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THE BALSAM WOOLLY APHID IN NEWFOUNDLAND

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ABSTRACT

The balsam woolly aphid, *Adelges piceae* (Ratz.), a serious introduced insect pest of balsam fir, *Abies balsamea* (L.) Mill., is expected to be a persistent problem of all susceptible forests in Newfoundland. Research information on the biology of the pest and the effect of infestation on individual trees and stands have been collected and integrated into a unified source of information. A damage hazard rating system based on site and stand parameters is provided and management procedures that may reduce losses from infestations are recommended.

RÉSUMÉ

Le puceron lanigère *Adelges picea* (Ratz.), un parasite non-indigène et nuisible au sapin baumier *Abies balsamea* (L.) Mill., s'annonce comme un problème tenace pour toutes les forêts prédisposées de Terre-Neuve. L'auteur présente, de facon intégrée, les résultats des diverses études sur la biologie du parasite et sur les effets de l'infestation sur des arbres individuels et sur des peuplements. Un système pour évaluer les risques de dommages, basé sur les paramètres des sites et des peuplements, est présenté, et l'auteur recommande des méthodes de gestion qui peuvent réduire les pertes occasionnées par les infestations.

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THE BALSAM WOOLLY APHID IN NEWFOUNDLAND

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H.O. Schooley and D.G. Bryant

INTRODUCTION

The balsam woolly aphid, *Adelges piceae* (Ratz.), an insect pest of balsam fir, *Abies balsamea* (L.) Mill., was accidentally introduced into Newfoundland, probably in the early 1930's. It was first recorded in the Province in 1949 shortly after which investigations including surveys and damage appraisals were initiated (Reeks 1949). In the early 1960's it became apparent that the infestation was spreading from western Newfoundland to other parts of the Island. Investigations were then expanded to include sampling techniques to measure population levels of the insect, biological and chemical control methods, and the effects of damage by the pest on individual trees and forest stands. Attempts to control the aphid by biological and chemical methods have failed and most of the susceptible forest stands in western, central and eastern Newfoundland have become infested. Many of the infested mature and semi-mature stands were killed by the hemlock looper, *Lambdina fiscellaria fiscellaria* (Guen.) during the outbreak of 1967-1970 and by the spruce budworm, *Choristoneura fumiferana* (Clem.) since 1972. As a result trees damaged by aphid are now less evident than they were formerly. Also, population levels of the insect are presently low in most infested areas. However, because balsam fir will continue to be a major component of Newfoundland forest stands, damage by the aphid will be a persistent problem and severe infestations will undoubtedly occur at periodic intervals. Recently most of the studies on the aphid have been terminated. Continuing efforts are primarily concerned with monitoring population levels and examining the long term impact of infestations in regeneration and semi-mature stands.

Results of research on the aphid are distributed in a number of reports and publications. This report is an attempt to integrate these results into a unified source of information.

THE INSECT

CLASSIFICATION AND DESCRIPTION

The place of the balsam woolly aphid in the scientific classification is as follows:

Class: Insecta
Order: Homoptera
Family: Phylloxeridae
Subfamily: Adelginae
Genus: *Adelges*
Species: *A. piceae* (Ratzeburg 1843)

Typically, in the family Phylloxeridae, there is more than one form of development. The balsam woolly aphid has two forms: sistens (plural: sistentes) and progrediens (pl.: progredientes). The more common (more than 97% of population) is the sistens form in which nymphs hatch from eggs and moult through three nymphal instars to the adult stage. The less common form, progrediens (less than 3% of population), has nymphs that moult through four nymphal instars to either a wingless or winged adult stage. The following descriptions of stages of development were adapted primarily from Balch (1952) and Varty (1956).

Sistens

Eggs: Eggs are oval to oblong in shape, 0.4 mm long and light brown in colour and each is attached to the bark surface with a filament produced by the adult at the time of oviposition. As embryos develop, the eggs become orange-brown in colour. Two eyespots and coiled stylets can be seen through the chorion.

First instar nymphs: First instar nymphs are about 0.4 mm long and hatch from the unattached end of the egg. At hatching they are orange-brown but over a period of about 10 days become purple-black as a result of melanization (Duewell et al 1950). A prominent fringe of flat whitish wax strands is produced around the sides and along the mid-dorsal line of the body. In addition, very short wax strands are produced at the trailing edge of each body segment. The body and antennae have many pegs, spines, spurs and plate areas, all of which are indicative of sense organs.

The first instar nymphs moult to the second and then to a third instar which are about 0.5 and 0.6 mm long, respectively. These nymphs, commonly called intermediate instars, produce a few wax strands from pores distributed over the body and turn purple-black in colour.

If these intermediate instars are hidden in crevices they usually remain brown in colour.

Adults: The adults are about 0.8 mm in length, hemispherical in cross-section, pointed at the posterior end, and coloured as the intermediate nymphs. The adults, however, produce a large number of wax threads that cover the body and a mass of eggs that accumulates at the insect's posterior (Fig. 1). When adults are hidden in crevices, wax threads are produced only on the side of the body not in contact with the sides of the crevice.

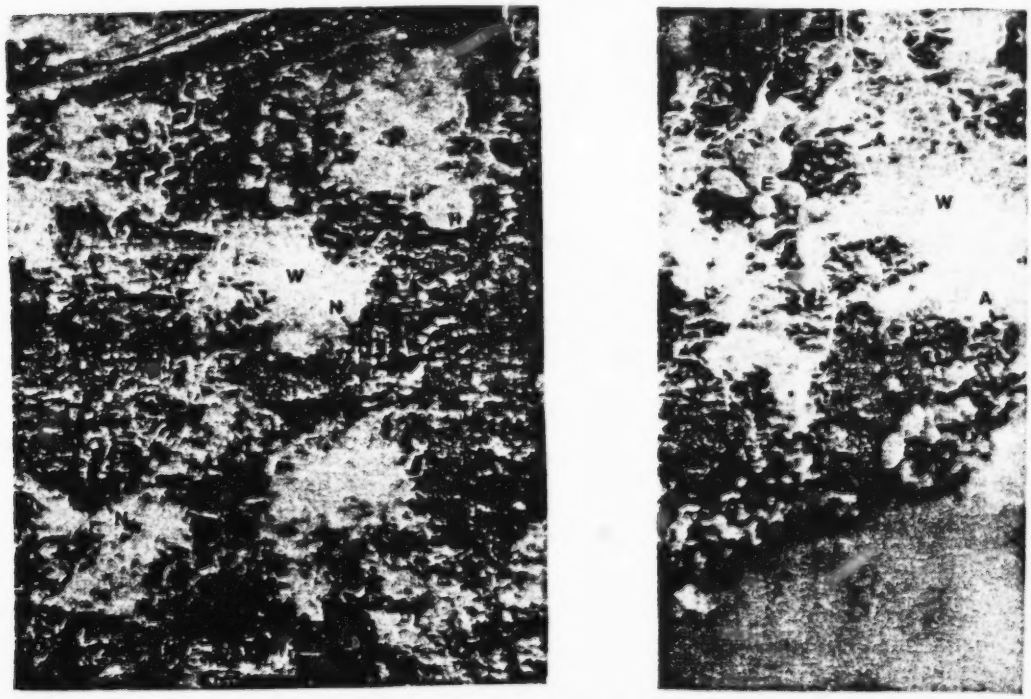

Fig. 1; Balsam woolly aphid eggs (E), first instar nymphs (N), and adults (A) covered by strands of wool-like (W) and globules of honeydew (H) excreted by adults on a twig of balsam fir.

Progrediens

Eggs: Eggs are indistinguishable from those of the sistentes.

First instar nymphs: First instar nymphs are about 0.4 mm long, oblong in shape, remain orange-brown at the posterior end, and are covered by a waxy bloom.

Other nymphal instars: The next three nymphal instars are coloured the same as intermediate instar sistentes but are more oblong in shape. Nymphs that develop into winged adults have wing pads on the top of the meso- and meta- thoracic segments of the third and fourth instars. The progredientes nymphs do not produce as many wax threads as the sistentes.

Winged and wingless adults: The wingless adult is about 0.8 mm long and the winged adult about 1.5 mm. The former is similar in shape to the sistens adult but the latter has a more robust thoracic region which bears the wings and contains the musculature and body sclerites needed for flight.

DISCOVERY AND DISPERSAL

Two areas infested by the balsam woolly aphid were found in Newfoundland in 1949 (Reeks 1949). A large infestation extending over 800 km^2 was present in the western part of the Island and is believed to have spread by wind from Nova Scotia in the early 1930's. A smaller infestation extending over 50 km^2 was present in and around St. John's, and is believed to have been started by aphids on infested European silver firs imported in 1920 for Bowring Park (Carroll and Bryant 1960). Many localized infestations have been found in other parts of the Island in subsequent years (Fig. 2) and the pest now occurs in over 16 000 km^2 of balsam fir forest from Port aux Basques east to St. John's and from Marystown on the Burin Peninsula north to Bonne Bay on the Great Northern Peninsula.

The aphid is a sedentary insect throughout most of its life but newly hatched first instar nymphs, called crawlers, can move considerable distances. About 20% of crawlers settle near the egg mass from which they hatch (Greenbank 1970). The remainder wander on the tree, either towards the apical end of branches or upwards on the tree stem (Bryant 1974). On warm sunny days, aphid crawlers tend to fall off the branch tips and may then be carried on rising convection currents to other trees in the stand or into the path of winds above the forest canopy (Edwards 1966). Transport of crawlers by wind is the major means of aphid dispersal. Sometimes, however, crawlers as well as eggs may be carried on the bodies of animals (Woods and Atkins 1967). The high

Fig. 2: Distribution of balsam woolly aphid and the dates of discovery on the Island of Newfoundland.

proportion of balsam fir in the forests across Newfoundland has provided a continuous belt through which the aphid could disperse. It is noteworthy that winds of 100 to 160 km/hour are common on the Island and that a major hatching period coincides with the equinoxal period of high winds in September.

LIFE HISTORY AND BIOLOGY

The life history of the balsam woolly aphid is complex because two forms are present in the population, more than one generation is produced each year, and reproduction is parthenogenetic (Bryant 1971). The sequence of the three generations shown in Fig. 3 applies to aphid populations in the majority of infested fir stands in Newfoundland. However, the number of generations may be reduced in cooler climates and at higher elevations, and they may be increased in warmer climates such as in British Columbia (McMullen and Skovsgaard 1972).

The development period of a generation varies with the season and form of development. Sistentes aphids develop from egg to adult in about 14 weeks in the summer generation which is present from June to October or early frost. Progredientes complete development in about eight weeks during June and July (Fig. 3). The overwintering generation, commonly called the spring generation, is present about 39 weeks.

The seasonal development of aphids in tree crowns is highly variable, and except during the winter period, it is difficult to find more than 80% of the population in one stage of development at a given time (Bryant 1971). Differences as great as 3 weeks in development can be found between groups of aphids only a few centimetres apart on the same branch. Aphids on the stems of trees tend to begin development later and complete it earlier in the season than those in the crowns of trees.

Adult sistentes usually oviposit 30 to 50 eggs but sometimes over 100 are laid. Wingless adult progredientes oviposit only a few eggs in the same location where they developed on the host tree. Winged progredientes have not been found to lay eggs in North America (Balch 1952; Bryant 1971) but oviposition by this form has been recorded in Europe (Varty 1956).

First instar nymphs (crawlers) hatch from the eggs about 10 days after oviposition. They then exsert the four parts of their stylets, which were loosely coiled inside the bodies, and by manipulating the rostrum and other mouth parts, they retract the stylets into the body joining them along their length to form a flexible feeding tube. The stylets are from 0.5 to 1.5 mm long and vary with the form and location of the aphids on the host tree and the age of the infestation (Balch 1952; Varty 1956; Greenbank 1970). The crawlers then wander over the

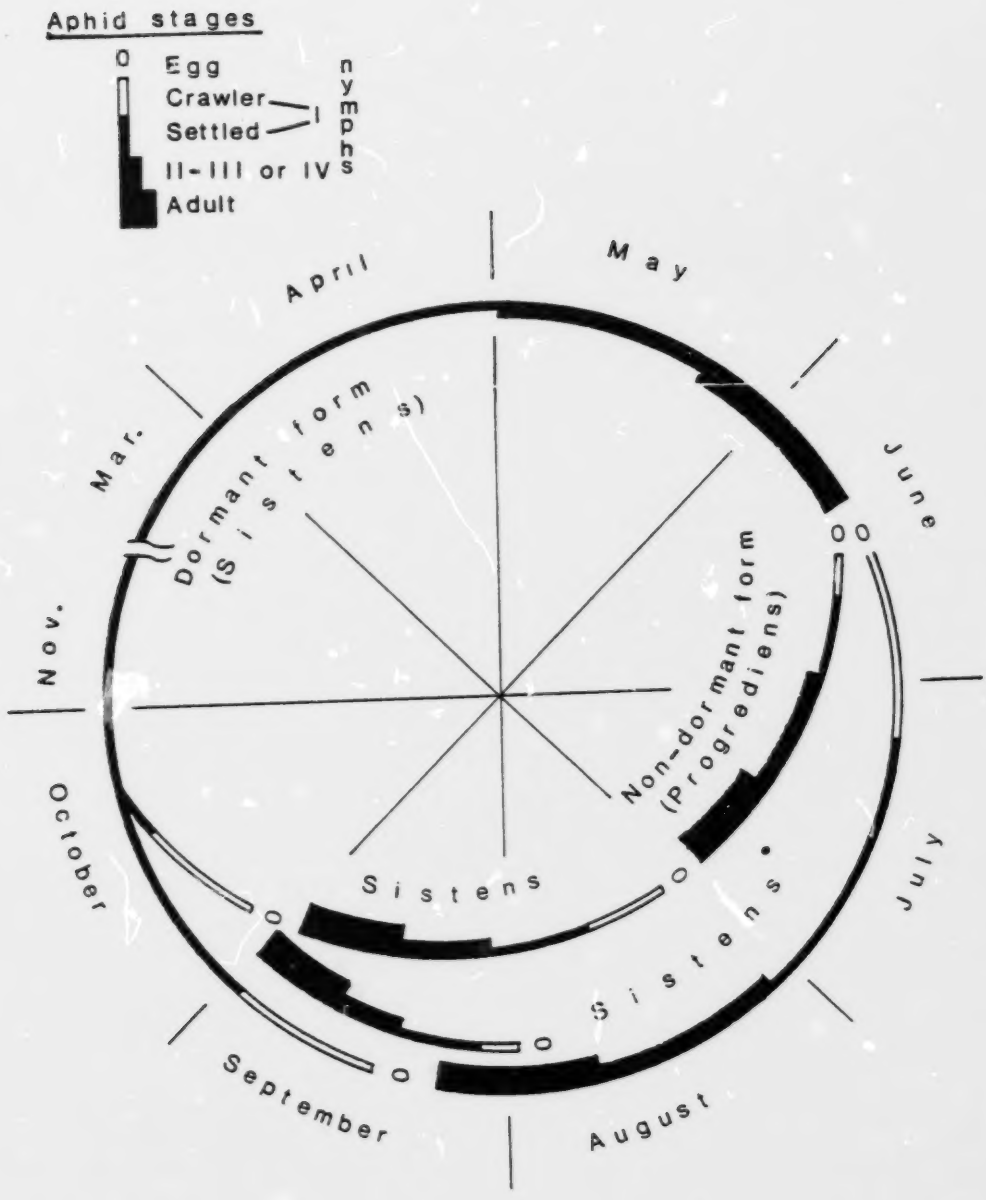

Fig. 3: Diagram of the life cycle and seasonal history of the balsam woolly aphid in Newfoundland. (Bryant 1976a).

bark surface until chemical tactile or some other stimulus induces them to stop wandering and insert their stylets into the bark (Balch 1952). Once the crawlers have inserted their stylets in the bark, they become virtually sedentary for the remainder of their life. The sistens aphids enter diapause at this time and the wax strands develop over the body surface apparently creating a favourable micro-climate for the insect. Following each moult, the feeding aphid inserts its new stylets into the bark near the previous insertion.

Progrediens aphids never exhibit diapause and in Newfoundland they have been found only on the branches of trees, primarily among the staminate flowers or strobili. The winged adults are found only among staminate flowers (Bryant 1971).

NATURAL FACTORS AFFECTING APHID NUMBERS

The reproductive capacity of the aphid is theoretically high because all individuals are female and lay eggs and there is more than one generation a year. Each spring generation aphid can give rise to about 2,800 aphids at the beginning of winter, but this potential is seldom if ever reached and population levels fluctuate between generations. The fluctuation can be caused by adverse or favourable weather, the condition of the host tree or the capabilities of the species itself. General climatic conditions are unimportant in determining population trends in Maritime regions such as Newfoundland because they do not restrict aphid development (Greenbank 1970). However, the factors related to weather are probably more important than any others in the increase of populations or in maintaining them at low levels. Weather is not a density dependent factor as it affects both high and low levels.

Late spring frost (temperatures less than $-2^{\circ}C$) can affect the survival of aphids, but its total effect is complex because of the variability in aphid development and the interaction of high aphid numbers with other mortality factors. In Newfoundland, aphids begin seasonal development during the last half of April, at least five to seven weeks before the hazard of late frost is past (Bryant 1971; Hemmerick and Kendall 1972). Individual aphids that developed early lay high numbers of eggs and produce progredientes. If there is no late frost, large increases in aphid numbers may occur. If there is late frost, many if not all early developing individuals are killed. The late developers escape the frost but tend to produce few eggs and no progredientes and as a result the increase in aphid numbers is minimal. The causes of varying reproductive capacity have not been fully determined but day-length, the quality of the host tree, and the genetic characteristics of early and late developing aphids are thought to be important factors.

Only first instar nymphs that have settled at a location, begun diapause and transformed to the black colour can survive the winter. All others are killed by the first frost of the autumn. An early frost will kill a high proportion of the population but if frost occurs late in the year, most of the aphid crawlers in the population will have settled. Of the aphids that settle on branches before the onset of winter, only 10% of those at the shoot tips and from 40 to 60% of those under the bud scales and at the flower buds may survive the winter (Bryant 1972). The remainder are apparently killed by low temperatures or possibly by dessication on warm winter days.

Aphid crawlers and, to a lesser degree, aphid eggs are dislodged from the host trees by wind and rain or are dessicated by the intense insolation of the sun (Atkins and Hall 1969). Bryant (1974) recovered only about 35% of the nymphs hatching from 4900 eggs placed on trees; the remainder were not found presumably because they were washed off the branches by rain.

The roles played by the condition of the host tree or the capability of the insect itself, in controlling aphid population levels, have not been studied. However, there is sufficient evidence to indicate that such controls certainly occur. For example, it has been observed that during a balsam fir flowering year, the reproductive capacity of the aphid population is high and numbers increase significantly (Bryant 1976a). Other observations indicate that an over-abundance of aphids on the host reduces its vigor and consequently the survival of aphids is also reduced (Balch 1952; Carroll and Bryant 1960). Further, mortality is frequently recorded among sistentes progeny of the spring generation. This mortality occurs when weather conditions are favourable for the development and survival of the aphid. Therefore, death may be associated with the vigor of the host tree or the viability of the aphid population (Bryant 1976a).

An indication of how aphid number levels fluctuate is obtained by measuring populations of successive generations. In Newfoundland, population data were collected from a variety of experiments undertaken between 1958 and 1975. The measurements for the adult stage of both the spring and summer generations are presented in Fig. 4. Both generations show similar trends in population levels. Insect numbers decreased in 1959 but increased to high levels in 1961 and 1962. They decreased to moderate levels from 1964 to 1966 after which they again fell and have remained low since 1971. The causes of these population fluctuations have not been fully determined, but some of the possible reasons are discussed in this report.

The data in Fig. 4 show that the abundance of spring generation sistentes adults was less than or equal to that of summer generation adults in seven of eight years in which both generations were measured. This relation was expected because mortality from weather was minimal or

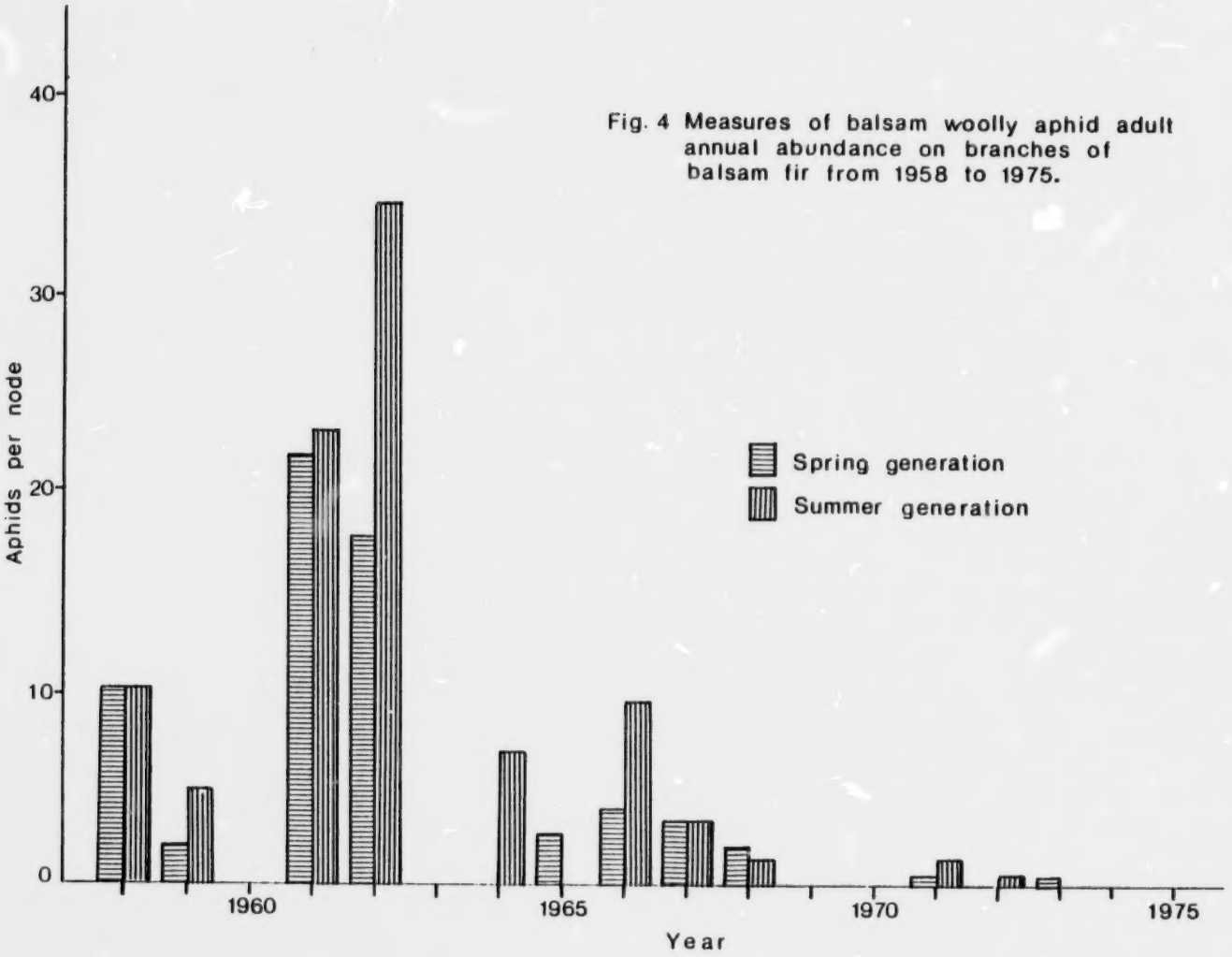

Fig. 4 Measures of balsam woolly aphid adult annual abundance on branches of balsam fir from 1958 to 1975.

absent and the incidence or effect of natural enemies was low in the second generation (Balch et al 1956). The size of the difference appeared to be associated with the amount of late frost in the first half of May each year. In 1962 and 1966 when large differences in aphid numbers were evident, there were less than three days of late frost (temperatures below -2°C). In 1958, 1959, and 1961, when there were small differences, there were five or more days of late frost in early May. It is possible that this late frost in May killed early developers, thereby reducing reproductive capacity. The relation of small or large differences to a high or low incidence of late frost in May did not persist after 1966 when populations remained at low levels.

MEASURING POPULATION LEVELS

SAMPLING FOR THE APHID

Sampling systems have been developed to detect new aphid infestations, to monitor population levels in existing infestations and to specifically measure population levels in relation to factors affecting aphid development or to evaluate control actions (Bryant 1976a, b). Both the stems and the crowns of balsam fir trees may be examined for aphids.

To sample for aphids on the stem, areas of bark surface of variable sizes have been used as sample units (Amman 1970). For example, in the Maritime Provinces of Canada population on 10 cm^2 of bark surface area are recorded as follows: heavy - over 32 aphids, medium - between 17 and 31 aphids, light - 1 to 16 aphids, and absent - no aphids present. In Newfoundland, the probability of high numbers of aphids on tree stems is low. The bark sample unit is appropriate for high population levels but is inaccurate for low population levels. Bryant (1976b) recommends that stem sampling should also include examination of lichen pads or thalli, lenticels and other crevices in the bark. However, a sampling system using these structures as sample units has not been developed.

To assess aphid population levels in the crowns of trees, it is most efficient to use counts of aphids located at nodes (Bryant 1976a, b). The node sample unit is the bark area bounded basally by the beginning of nodal swell and apically by the bud scales that are covering the base of the shoots (Fig. 5). In the node area, aphids are found most often under and between the bud scales. The sample unit for tree crowns is a node located in the second position on the secondary twig of a balsam fir branch (Fig. 5 node #8, 12, 17 or 30). This node position was selected because aphid numbers vary in a consistent manner. Node samples should

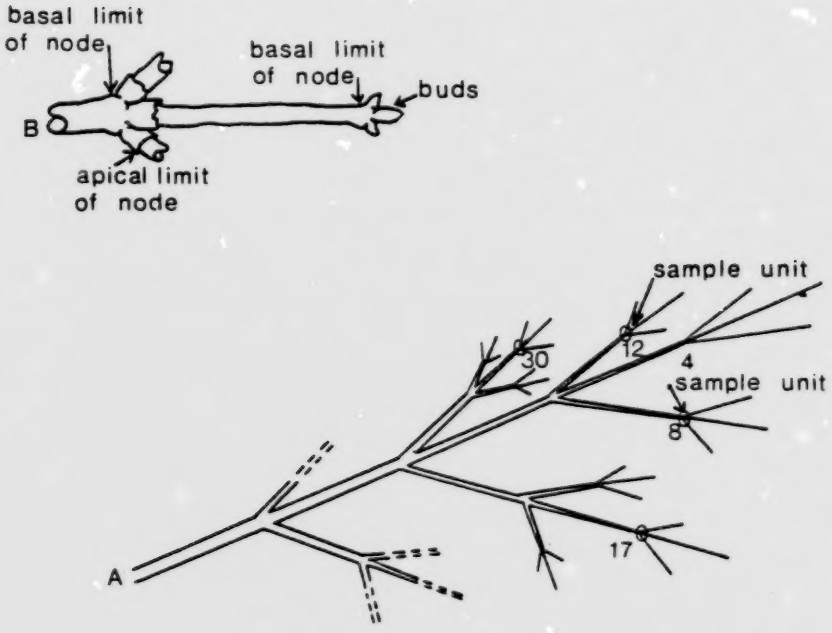

Fig. 5: A. Diagram of a 5-year-old branch showing the location of sample units, second position nodes no. 8, 12, 17 and 30
B. Details of shoot, showing node limits (Bryant 1974).

be taken from among 4- to 12-year-old branches of semi-mature and mature trees, 3- to 8-year-old branches of trees about 5 years old at breast height and 3- to 5-year-old branches of younger trees. The branches sampled should not have male flowers in the apical three years of growth unless it is known that only low aphid populations are present on the trees.

DETECTION

Detection surveys are conducted simply to determine the presence or absence of aphids. Node samples are examined with the aid of a 6X to 10X hand lens. Only one node is collected per tree and the number of trees that must be sampled at a location varies with the number of locations to be sampled in a stand (Table 1). It may be prudent to sample one location for every 10 hectares of forest. A stand can be classed as uninfested with 95% confidence if all prescribed sample units do not bear aphids. As soon as an aphid is found, the stand is classed as infested.

Table 1.- The number of sample trees required per sample location allocated at one per 10 hectares to state with over 95% confidence that a balsam fir stand is uninfested by the balsam woolly aphid (Bryant 1976b).

Number of locations in a stand	Number of trees per location
1	5
2	6
3 to 5	7
6 to 10	8
11 to 16	9

This sampling system for detecting aphids in tree crowns was developed for first instar nymphs only. Accordingly, sampling in Newfoundland must be done between October 10 and May 10 for the over-wintering generation and between June 25 and July 30 for the first summer generation.

To determine if aphids are present on the stems of trees, the bark beneath at least four lichen pads (thalli) per tree should be examined. However, if aphids or wool spots are evident on the exposed bark of the stem, further examination is not warranted to class a tree or stand as infested.

MONITORING

The monitoring of aphid population levels is necessary to detect the beginning of outbreaks over extensive areas and to determine changes in the condition of outbreaks. Analysis of population behaviour and distribution in trees showed that low hazard, non-damaging population levels were present where less than about one third of the node samples from tree crowns were infested (Bryant 1972). If more than 33% of the node samples were infested, then potentially damaging numbers were present and further sampling would be necessary to determine if immediate control action was required. The sampling intensity described for detection surveys (Table 1) can be used for monitoring known infestations.

Methods for measuring population levels in tree crowns have been developed (Bryant 1976b). The required number of samples for prescribed allowable error, confidence level, and assurance are shown in Table 2 for high and low population levels respectively. If the variance of the sample exceeds 0.2000 then the population level is high; if less than 0.2000 then population level is low.

The sample sizes given in Table 2 were developed from formulae given by Li (1964) for single estimates and comparison of two means (treatments). To compare more than two means, formula to calculate appropriate sample sizes may be obtained from Li (1964), Federer (1955) and Steel and Torrie (1960).

More than one node sample unit may be collected per tree crown, but no more than one sample unit should be taken from a branch at a sample time.

The system may be applied to any sedentary stage or phase of the aphid such as the diapausing, feeding or ovipositing aphids. It is not appropriate for crawlers, which are motile, or for eggs, which are grouped in clusters near their parent. If sampling intensity must be reduced because of limited time or resources then the number of sample units can be decreased to a minimum of 20 nodes. However, the accuracy and assurance of the estimates are also reduced.

DAMAGE TO FOREST TREES AND STANDS

DESCRIPTION AND CLASSIFICATION OF DAMAGE

Damage to balsam fir trees caused by the balsam woolly aphid is distinct and unlike damage caused by other forest insect pests. The main stem of balsam fir in the inland areas of the Northeastern United States of America and New Brunswick may be infested with large numbers of aphids (Fig. 6). In Maritime areas, such as Newfoundland, attack is usually concentrated in the crowns of trees (Fig. 7).

Table 2.- Number of sample units (nodes) required in a high or a low population level of aphids to estimate each mean with a confidence of 90 or 95 percent at an allowable error of 10 to 33 percent of the mean with an assurance of 0.75, 0.90, or 0.95.

Allowable error[a]	Estimate one mean			Compare two means		
	Level of assurance					
	.75	.90	.95	.75	.90	.95
High aphid population level (S^2 = 0.257971 at 40 df.)						
90% confidence						
.08	138	163	177	271	302	332
.11	79	94	102	148	172	184
.20	26	33	36	46	55	59
.26	18	20	21	32	37	39
95% confidence						
.08	192	222	244	375	428	466
.11	109	119	131	199	237	258
.20	38	41	44	64	82	93
.26	23	29	32	39	47	52
Low aphid population level (S^2 = 0.042904 at 48 df.)						
90% confidence						
.03	166	187	199	313	378	410
.05	59	74	84	117	136	152
.07	31	38	41	60	71	86
.10	18	22	24	31	38	41
95% confidence						
.03	228	265	283	457	500	546
.05	92	105	112	170	191	201
.07	44	54	57	72	84	113
.10	24	29	31	44	53	57

[a]Nominally 10%, 15%, 25%, and 33% of the mean.

Fig. 6: Wool-like wax threads excreted by heavy infestation of aphids on the mainstem of trees.

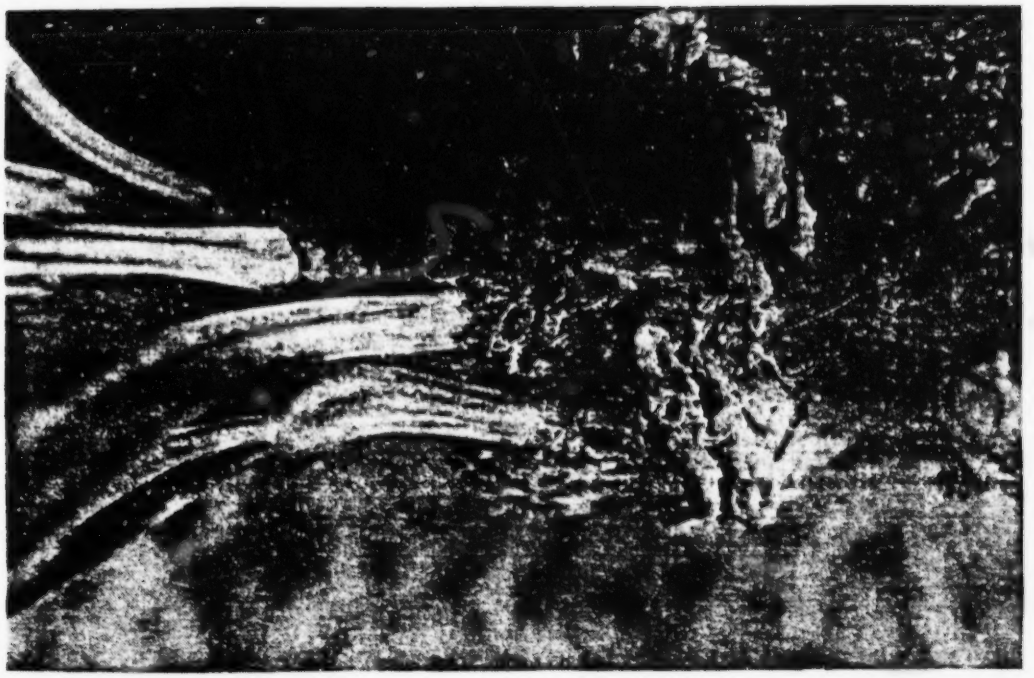

Fig. 7; Aphids on a shoot from the crown of an infested tree.

The Initiation of Damage

The aphid is a sucking insect. It inserts its stylets intercellularly through the bark epidermis into the cortex and the parenchyma tissue. Pectinase activity in aphid saliva that could dissolve the pectin bonds between cells and allow probing by the stylets is reported (Adams and McAllan 1958). Some physical disturbance or injury of cells occurs as the aphid feeds and the withdrawal of food from the tissues by the aphids undoubtedly is also detrimental to trees.

Injury is thought to originate as a result of the disruption of the natural hormonal balance that controls the growth of trees. This disruption is evidently caused by a salivary substance ejected during feeding (Balch 1952). Aphid saliva may contain growth regulating hormones. However, it is more probable that localized enzymatic or synergistic action by the saliva with constituents of the tissues near or penetrated by the stylets, produces either abnormal quantities, or enhances the activity of growth-regulating substances already in the trees (Balch, Clark and Bonga 1964). This hypothesis is reasonable because both a growth-promoting auxin, indole 3-acetic acid (IAA) and a growth inhibitor, β-inhibitor, are found in the bark of balsam fir (Bonga and Clark 1963, 1965). The effects aphid feeding have on xylem tissue were stimulated by the application of IAA in lanolin co an area of bark after it had been scarified (Balch 1952). Studies show that β-inhibitor is more abundant in the bark of trees attacked by the aphid than in uninfested trees (Bonga and Clark 1965). Tissue malformations resembling those formed by aphid attack are obtained in laboratory tests of this inhibitor on bark cultures. Although it seems evident that aphid damage is caused by saliva disrupting the natural hormonal balance in trees, the way in which this is accomplished will probably remain unknown until the saliva itself is isolated and analysed and the sequence of reactions are determined.

Physiological Changes

Aphid attack severely upsets the metabolic functions of infested trees. Various workers identify drought-like conditions at the tops of trees indicating that the aphid adversely affects water conduction. Studies using dyes show that there is a marked reduction in liquid movement through the xylem in parts of trees affected by aphid feeding (Balch 1952; Mitchell 1967a). In contrast to unaffected trees, the dye in affected trees is transported in narrower bands of early wood in fewer growth rings and does not ascend as high (Mitchell 1967a). The permeability of the sapwood in aphid infested grand fir is only 5 percent of that in normal sapwood. This reduced level is about equal to the permeability in normal heartwood (Puritch 1971). The reduced water transport is caused by the encrustation of the bordered pit membrane pores in xylem tracheid cells (Puritch and Petty 1971; Puritch and Johnson 1971).

Puritch (1973), by depriving balsam fir seedlings of water, determined that water stress affects photosynthesis, respiration and transpiration. Net photosynthesis, after an optimum rate, changes in three phases as water stress increases; viz., a rapid rate of decline, a second more gradual reduction, and finally, a steady state of zero net photosynthesis. Both respiration and transpiration begin to decline at about the same level of water stress as photosynthesis, but respiration declines to about 40 percent and transpiration to about 10 percent of their initial rates. On the basis of this information, it is postulated that decreased water transport caused by aphid attack can produce drought conditions resulting in decreases in photosynthesis, respiration and transpiration.

On European fir the areas of bark attacked first by aphids are those where the tissue protein content is naturally the highest; viz. near lenticels or bark fissures (Kloft 1957). Continued feeding in these areas increases the protein levels of adjacent tissues and this proliferation of protein leads to the successful establishment of aphids at locations other than those occupied initially. However, after a period of infestation the fed-on tissues become exhausted, the cells die and are no longer suitable for aphid feeding.

The number of cellular protoplasmic starch granules decreases in European fir as the period of aphid feeding increases (Oechssler 1962). Measurement at various times of the year show that the total carbohydrate, starch and sugar contents of the twigs and foliage of aphid infested grand fir are less than those found for undamaged trees (Puritch and Talmon-de L'Armée 1971). It should not be concluded that aphid saliva contains polysacharide-splitting enzymes but it is probable that aphid-caused reduction of water transport and the resultant water stress condition are detrimental to carbohydrate metabolism.

Cellular and Tissue Changes

The cortical tissues in which the aphid feeds include the annual phelloderm layers, the medullary rays and the epithelium of resin canals. In the bark of the stems and young shoots of balsam fir, the aphid stylets occasionally reach the phleom but do not enter it. However, stylet tracts are seen in the meristematic tissue at the base of buds (Balch 1952). The parenchyma cells adjacent to the paths followed by the stylets of feeding aphids are enlarged (hypertrophy) with thickened walls and large or multiple nuclei. The number of parenchyma cells near the probed areas are increased (hyperplasia)(Balch, Clarke and Bonga 1964). This additional volume of the parenchyma causes swelling of the bark, especially on young twigs.

The initiation of wound healing in affected trees is indicated by the formation of reddish-purple secondary periderm cell layers around or beneath the abnormal parenchyma tissues (Balch 1952; Mullick and Jenson 1972). Small groups of dead or dying parenchyma cells are surrounded by secondary periderm, and then infiltrated with resin to form the periderm pockets often found in the bark of twigs that have been infested by the aphid. Heavily infested stems may develop a secondary periderm beneath areas of affected parenchyma and this layer protects the living bark under it from further attack.

The cambium beneath the aphid-affected bark is stimulated by aphid feeding to produce a localized enlargement of the xylem ring basipetally from the point of feeding (Balch 1952). The abnormal xylem is called "redwood". Redwood tracheids are histologically similar to those of compression wood. They have thickened, spirally checked secondary walls with large fibril angles, a reduced lumen, a circular rather than rectangular cross-section and reduced length (Figs. 8 and 9). Xylem affected by the aphid also has a greater number and larger vacular rays and more numerous parenchyma strands than normal xylem (Mitchell 1967b, Smith 1967).

Structural Changes

The physiological, cellular and tissue changes that occur in response to aphid attack result in peculiar structural developments in affected trees. These developments include abnormal or reduced radial growth and elongation by main stems and branches and malformation of various parts of the trees. Dieback of tree crowns and possibly premature death of trees may follow.

Usually, an abnormal drooping of current shoots is the first visual symptom of aphid attack (Fig. 10). This symptom resembles the drooping that occurs when fast growing, succulent new shoots are unable to support their own weight. Aphid feeding at the basal nodes of new shoots causes them to droop and prevents them from regaining the near horizontal, normal position so that the droop becomes permanent. Drooping shoots are usually formed each year as long as the tree remains infested. After several years of heavy infestation the main stem at the tops of trees frequently tilt to assume a near horizontal position (Fig. 11).

The swelling of branches, particularly at the nodes, a characteristic of trees with aphid-infested crowns, is termed 'gout' (Fig. 12). Gout development is initially most common on the 5-year-old branches (Fig. 13) but is found throughout the crown on severely damaged trees (Schooley and Oldford 1974b). Continued feeding by the aphid results in an accumulation of the swelling effect on both the nodes and

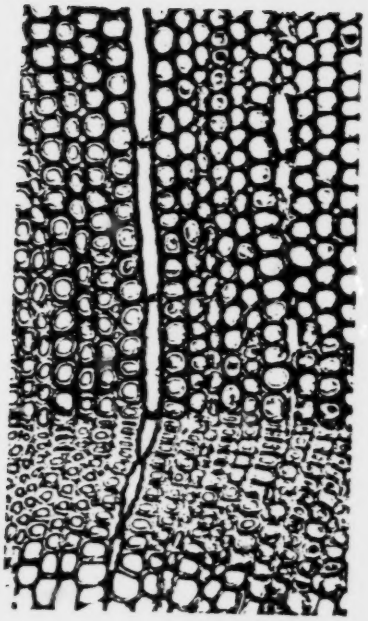

Fig. 8; Transverse section from stem of infested tree. Note circular cross section and intercellular spaces. X130, (Balch 1952).

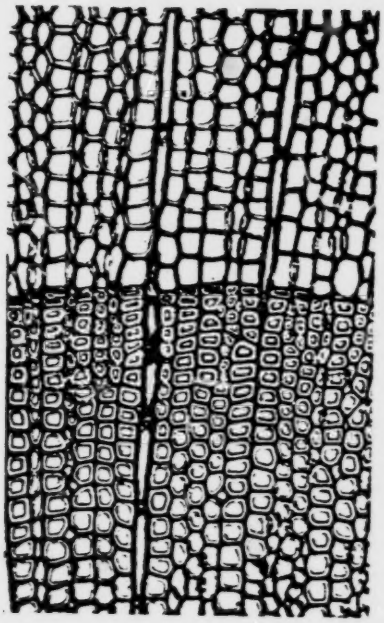

Fig. 9; Tranverse section of normal stem wood. Same tree as Fig. 8 but taken from wood laid down before infestation, (Balch 1952).

Fig. 10; Abnormal drooping of shoots in the crowns of trees indicates aphid infestation.

Fig. 11; Extensive swelling and loss of foliage resulting from aphid attack.

Fig. 12; Swelling at the nodes of branches "gout" as a result of aphid feeding.

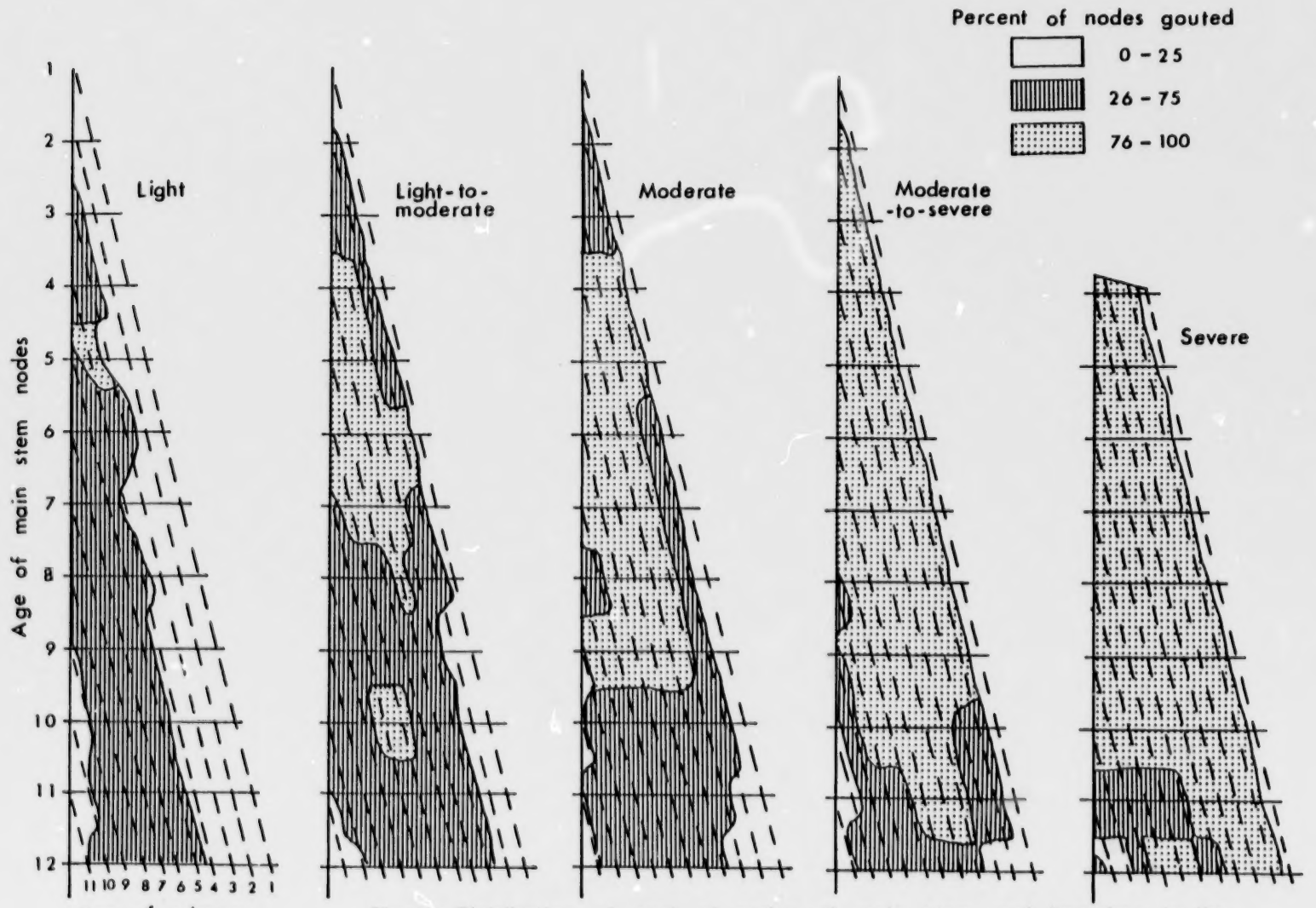

Fig 13; Distribution of gout at nodes of main stem and branches in the upper 12 years of balsam fir trees in five damage classes (Schooley & Oldford 1974b).

internodes at the periphery of branches. Branch tips become club-shaped with their buds almost enclosed in knobs of tissue. Needles are lost from these areas of extensive swelling so that shoots become partially or completely defoliated (Fig. 11).

Several studies indicate that in addition to gout the number and length of branches and the length of the main stem are reduced by aphid attack (Balch 1952; Warren, Parrott and Cochran 1967; Schooley 1974b). Reduction in linear growth occurs first in the branches and then in the main stem of trees. Continued infestation causes stem and branch elongation to decrease each succeeding year; after several years of attack elongation ceases. This cessation may be brought about by a lack of bud production but more probably occurs because the buds fail to flush. Aphid attack first causes a decrease in twig numbers, followed by a decrease in branch numbers and then main stem production stops. Failure to produce branches reduces the foliar volume of the crown and consequently must adversely affect photosynthetic production by the trees.

The radial increments of wood in the main stems and branches of aphid-attacked trees may increase for several years because the growth of xylem is stimulated to form redwood. At the same time as abnormal xylem is being produced, the volume of bark parenchyma is also greatly enlarged, and the combination of these two developments increases the overall stem and branch diameter. In places on the stem where aphid feeding has been concentrated, such as at lenticels and bark fissures, the bark surface may bulge outward because of increased tissue production. After a few years of enhanced growth, the width of annual rings may be greatly reduced (Fig. 14).

The most advanced stages of aphid damage found are top killing, dieback and tree mortality (Fig. 15). Up to 14 years of growth may be killed on the tops of severely damaged mature trees (Schooley and Oldford 1974b, Warren, Parrott and Cochran 1967). On young trees as much as seven years of terminal growth may be killed (Schooley 1976a). All trees show a reduction in stem elongation before dieback occurs. Persistently high stem populations may cause the death of trees within two or three years without much external evidence of damage. However, this form of attack and the resultant mortality are not common in Newfoundland. Trees damaged by high numbers of aphids in the crown may also die (Schooley and Oldford 1974a; Warren, Parrott and Cochran 1967). Damage is easily seen but mortality occurs only when the attack persists for several years. The probability of death from crown attack is lower for vigorously growing regeneration and semi-mature trees than for less vigorous mature and overmature trees.

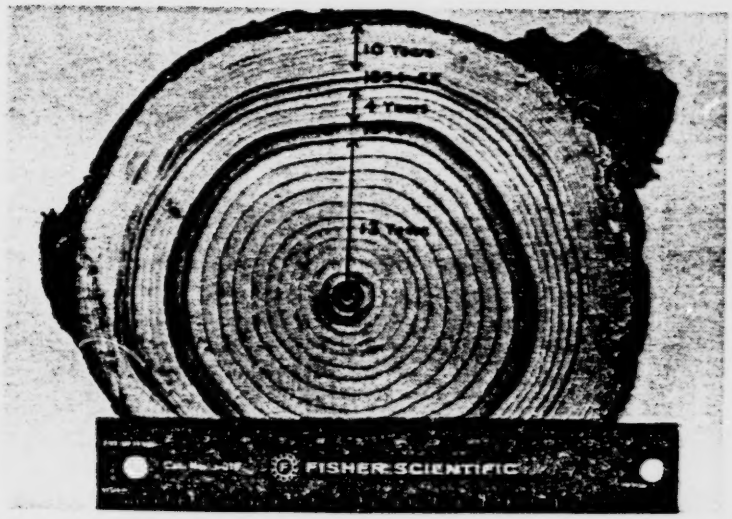

Fig. 14; Stem disc from a severely damaged balsam fir. The wide darkened rings are composed of redwood.

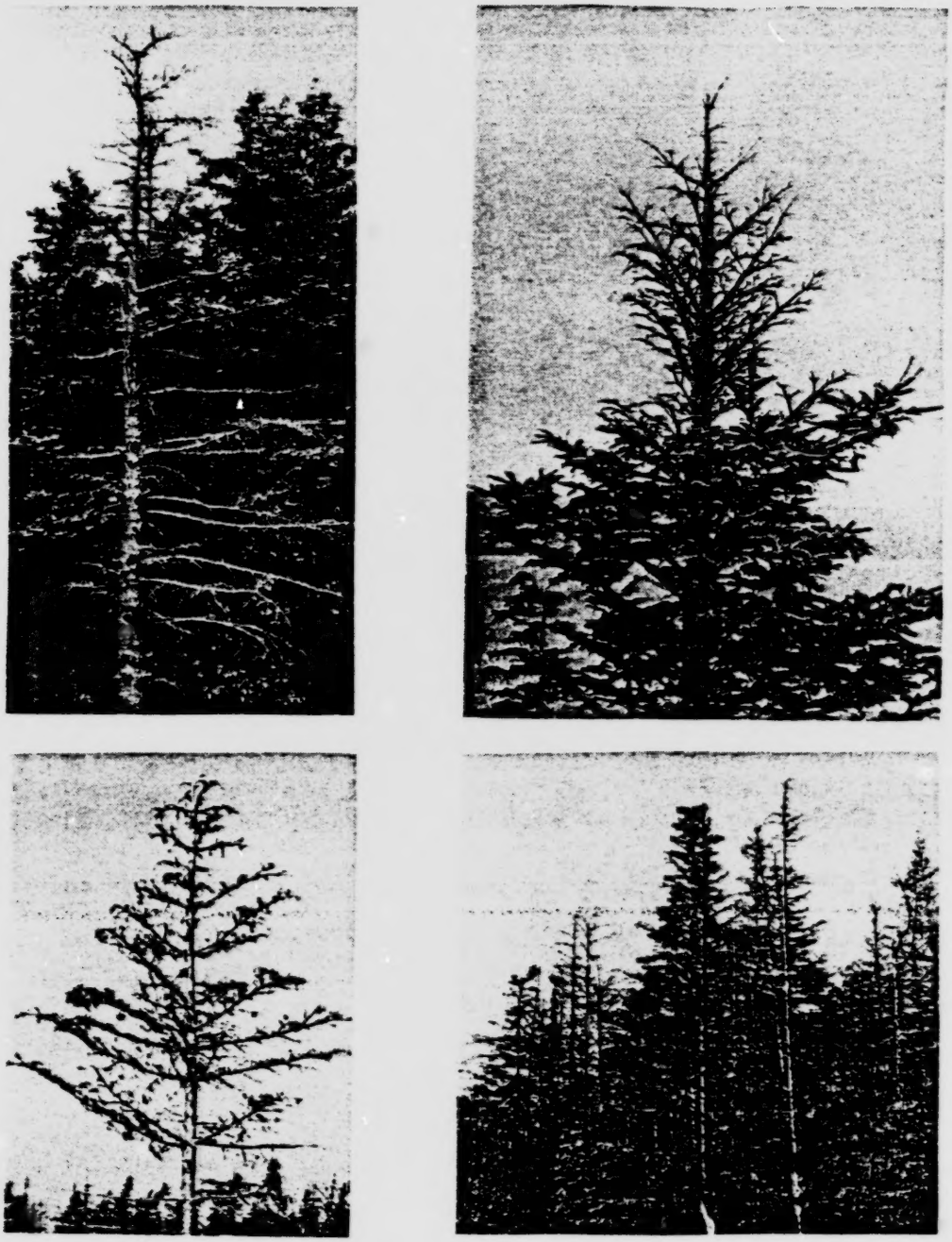

Fig. 15; Advanced stages of aphid damage, top killing, dieback and mortality.

Recovery

The amount of injury to trees is influenced by their inherent resistance as well as by the severity and duration of infestation (Balch 1952; Balch and Carroll 1956). When an infestation subsides, damaged trees may recover. Recovery may be permanent, but more often it is temporary because trees may become reinfested and pass through several cycles of damage. Damage from renewed aphid attack is greater and develops more rapidly on young trees that have previous severe damage than on trees with previous light damage (Schooley and Oldford 1974a).

Increased production of shoots that are normally oriented instead of drooped, particularly on young trees, is a good indication that aphid infestation has subsided and recovery has started (Fig. 16). The recovery of top killed trees sometimes proceeds with strong lateral growth but without successful vertical development. This results in the top of trees becoming flat or club-shaped (Fig. 17). When renewed main stem growth occurs on top killed young trees, it usually begins with the reorientation of a branch to the vertical position (Fig. 16). Deformities resulting from this reorientation are soon overgrown (Schooley 1976a). Recovery is less striking on lightly damaged trees where only minor changes in the growth pattern are necessary to return to normal. In a few years after the initiation of recovery most of the readily apparent symptoms of attack such as gout and defoliation are overgrown and difficult to detect. With increased foliage production, radial increments of wood may increase on trees that have shown reduced growth because of aphid damage (Warren, Parrott and Cochran 1967). Most young trees react favourably to release from infestation and show an immediate return to normal radial and height growth (Schooley 1976a).

Damage Classification

Trees may support a small population of aphids without damage being apparent. At high population levels the wool-like wax threads secreted by the insect are seen as white spots on the bark surface and the symptoms of attack become evident as structural changes described above occur. On the stems of trees the number of wool spots has been used to assess the severity of attack because damage is not readily apparent on the trees. Aphid damage occurring in the crowns of trees is classified by the sequence in which the various symptoms of attack become apparent. Initially there is a swelling at the nodes, then a deformation of shoots, followed by tip inhibition, defoliation and dieback. An outline of the classification system as adapted from Warren, Parrott and Cochran (1967) follows:

Fig. 16; Normally oriented recovery growth and branch reoriented to form a new leader on young severely damaged tree.

Fig. 17; Flat top and club shaped top of trees as a result of recovery growth.

Damage Class	Description	Numerical Code
Undamaged	Normal branch, no visible symptoms of attack	1
Light damage	Node swelling indistinct, apparent only at close examination	2
Light to moderate damage	Node swelling distinct, some stunting or distortion present	3
Moderate damage	Distortion prominent, branch tip inhibited, thinly foliated	4
Moderate to severe damage	As in moderate but terminals and some branches bare from tips up to 30 cm or up to one-half the length of short branches	5
Severe damage	As in moderate but terminals and some branches bare for more than 30 cm or more than one-half the length of short branches	6
Dead trees	Inner bark brown at breast height and symptoms or signs of aphid attack present	7

Living trees may recover from all levels of aphid damage. For this reason trees are often described in terms of the level of damage that was present before recovery started, e.g. recovered from moderate damage. A numerical code is available for each level in the classification to facilitate record keeping. Observations indicate that periods of damage accumulation alternate with periods of recovery. These cycles, and the extent of damage in each cycle, may be recorded by a damage number of one or more digits which indicates the number of cycles apparent in the tree.

This classification is used to record the level of crown damage in several ways. In general surveys and regeneration studies all trees are placed in the class designated by the most serious symptoms present anywhere in their crowns (Schooley and Oldford 1974a). In aphid population studies, the most severe level of damage in the subapical quarter of tree crowns is recorded. More aphids and greater damage occur here, especially on trees showing low levels of damage or those recently infested (Bryant 1976a). Assessments of aphid impact and deterioration studies are based on the damage throughout tree crowns. The upper and lower crown halves are each classified by the level of damage indicated

by the most prevalent symptom, and then the numerical values of these levels are averaged to obtain the level of damage for each tree (Page 1973) as follows:

Range of mean numerical code (X)	Average damage to a tree
$X = 1$	no damage
$1 < X \leq 3.0$	light damage
$3.0 < X \leq 4.5$	medium damage
$4.5 < X \leq 6.0$	severe damage
$X = 7$	dead

The above classification system qualitatively stratifies trees, by their appearance, into damage classes. However, the number of branches and the amount of main stem and branch growth varies significantly among classes (Schooley and Oldford 1974b; Bryant 1972). These differences suggest that quantitative measures may be developed to replace the subjective criteria now used for stratifying trees damaged by the aphid.

In Newfoundland, damage surveys are used to detect new areas of aphid infestation or extensions to the boundaries of existing infestations and to appraise the amount of damage being done. The detection of balsam woolly aphid infestations requires observations of large forested areas, many of which are inaccessible by road. Aerial examination followed by ground observation where possible, has been the best way to achieve maximum coverage at minimum cost. Both fixed-wing airplanes and helicopters are used in these aerial detection surveys (Warren, Parrott and Cochran 1967). The aerial surveys were particularly useful in establishing the extent of infestations when the insect was first discovered (Carroll and Bryant 1960) and for identifying severe damage and mortality in areas known to be infested. However, aerial surveys have been ineffective for detecting the initial stages of newly developing infestations and for recognizing renewed aphid activity in forest stands that have recognized by ground surveys. Ground surveys to detect damage are most successful when made in the spring, late summer or fall. They are less accurate if conducted in June or July when new shoots are limp or in the winter when branches are laden with snow.

Aerial photography has been used to appraise damage by the balsam woolly aphid. Bajzak (1966) found that in Newfoundland different damage conditions of trees (undamaged, light to moderate damage, severe damage and dead) could be interpreted most accurately on 1:720 scale Ektachrome Infrared Film. He recommended that appraisal of damage by injury classes and volume losses should be carried out using 0.04 ha ground and photo plots on large scale photography. Elsewhere in North

America, it is generally concluded that for extensive areas, good estimates of severely damaged and aphid killed trees can be obtained from aerial photographs for a much lower cost than from ground surveys (Aldrich and Drooz 1967; Heller et al 1967). However, photographs are not suitable for mapping infestations where mortality has not occurred, or for mapping year to year infestation changes. Aerial detection and appraisal surveys and aerial photography are most useful when conducted in the mid-spring after the snow has melted but before the hardwood trees become foliated.

The information collected by damage detection and appraisal surveys is used to determine changes in the status of damage, to indicate trends in the development of damage, and to help minimize the losses from mortality and cull by indicating where sanitation and salvage cutting operations are required.

THE EFFECTS ON INDIVIDUAL TREES

Reproductive Potential

Balsam fir trees begin to produce seed at about thirty years of age. The cones are usually produced on a two-year cycle, regularly alternating between heavy and light crop years (Schooley 1975). Cone production is greatest on open grown or dominant and codominant trees in stands. Seed is released when the cones break up in early autumn. Most seed falls near the parent tree (Hall and Richardson 1973).

Differences in cone production for a heavy crop year on sub-merchantable fir trees having various levels of aphid damage are shown by Schooley (1975). A comparison with records taken for the previous heavy crop year, when all but the severely damaged trees were unaffected by the aphid, indicates that an appreciable decrease in cone production occurs on trees that have sustained moderate or greater aphid damage (Table 3). The latter trees have fewer cones because aphid attack reduces or eliminates the growth of cone-producing shoots. Schooley (1976b) also shows that cone size, the quantity and quality of seed and the amount of damage from cone insects are not correlated with aphid damage at any level. Because serious damage does not occur on all trees simultaneously, and because the seed produced is unaffected by aphid injury, it is concluded that adequate seed for stand replacement is available from balsam fir trees damaged by the aphid. This conclusion is supported by subsequent surveys that found dense stands of fir regeneration in areas where the parent stands had been severely damaged by the aphid (Schooley and Oldford 1974a).

Table 3.- Total cone production and cone production on main branches, means ± standard deviations for 1964 and 1960 on trees in six balsam woolly aphid damage classes.

Damage class in 1964	No. trees examined	Cones per tree		Cones on main branches per tree	
		1964	1960	1964	1960
Undamaged	10	87 ± 34	68 ± 48	56 ± 27	53 ± 34
Light	9	90 ± 67	57 ± 40	53 ± 48	39 ± 28
Light-to-moderate	7	70 ± 36	79 ± 51	37 ± 25	46 ± 31
Moderate	7	75 ± 39	77 ± 58	41 ± 26	60 ± 52
Moderate-to-severe	8	19 ± 22	82 ± 40	13 ± 16	52 ± 41
Severe	8	4 ± 5	37 ± 32	2 ± 3	18 ± 17

Height, Diameter and Volume

The normal growth and dimensional relations of balsam fir are essentially functions of the physiology, cellular and tissue constituents, and structural organization of the species. Height and diameter growth, stem form, height/diameter relations, and crown dimensions are all altered to varying degrees by different levels of aphid attack.

In 8- to 15-year-old trees in western Newfoundland, height growth was up to 47 cm less over a 6-year period on moderately and severely damaged trees as compared to undamaged and lightly damaged trees of the same initial height (Fig. 18). Growth losses of this order can cause affected trees to lose their place in the canopy and become suppressed (Fig. 19). However, recovery growth is a common phenomenon in young stands and normal height growth usually returns on reactivated leaders or reoriented branches after infestation has subsided (Schooley 1976a). Older, severely damaged trees are often from 1.5 to 3 m shorter than undamaged trees of equivalent diameters (Page, Schooley and Hudak 1970). In general, the older the tree the less likely it is that normal height growth will return upon recovery.

Volume tables constructed for aphid damaged trees from western Newfoundland (Page, Schooley and Hudak 1970) show that there are significant differences in merchantable volume contents between damaged and undamaged trees of equivalent diameters (Fig. 20). In general trees in the moderate damage class have greater volumes than comparable undamaged trees, while

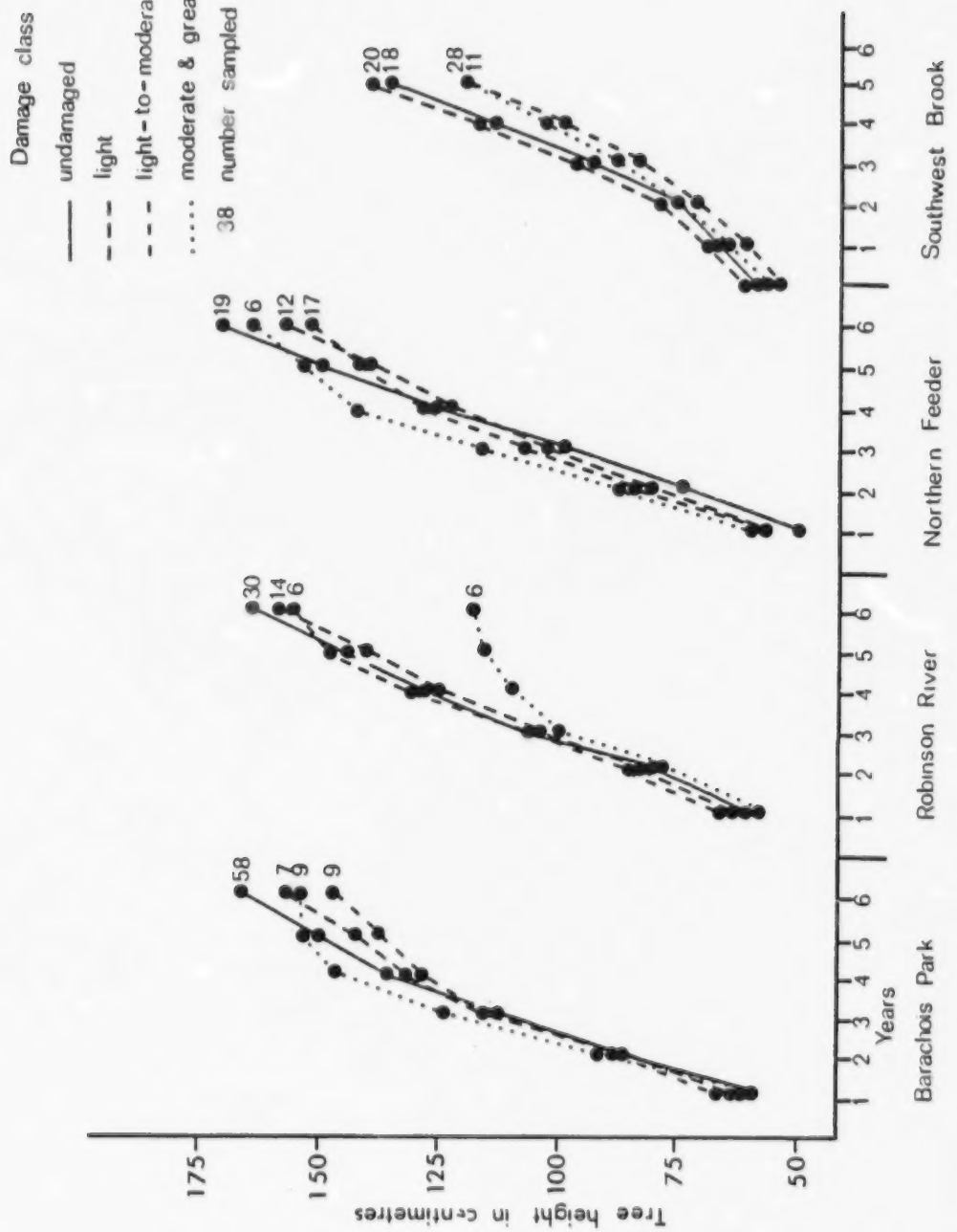

Fig. 18. Effect of aphid damage over a six year period on the height growth of trees that were initially 0.6 metres tall.

Fig. 19: Aphid damaged trees may become suppressed as a result of reduced height growth.

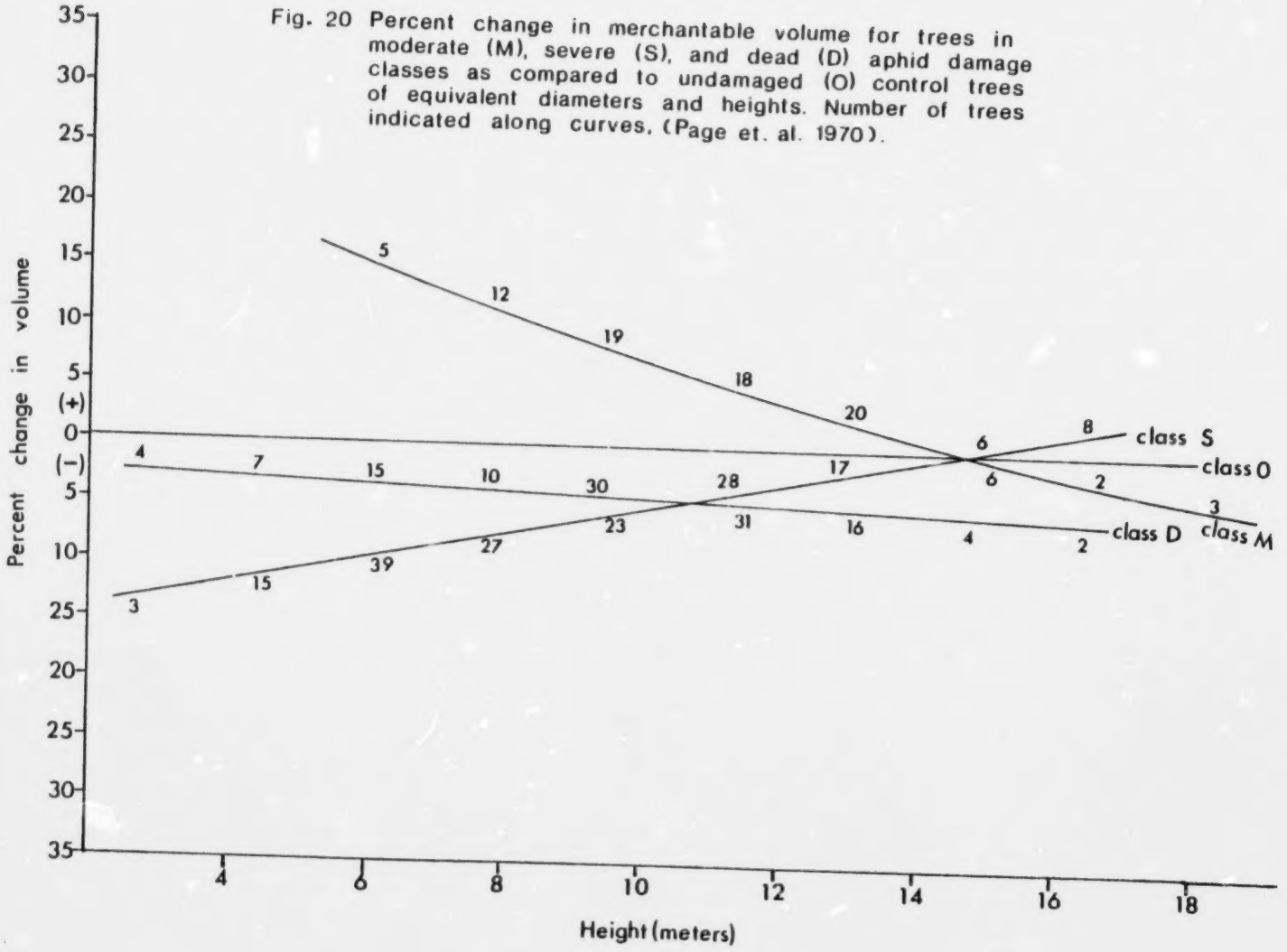

Fig. 20 Percent change in merchantable volume for trees in moderate (M), severe (S), and dead (D) aphid damage classes as compared to undamaged (O) control trees of equivalent diameters and heights. Number of trees indicated along curves. (Page et. al. 1970).

those severely damaged or killed by the aphid have lower volumes. Lightly damaged trees show no significant differences from undamaged trees in terms of their volume contents.

The differences in volume content in the moderate, severe and aphid-killed damage classes appear to be associated with alterations in tree form resulting from differential growth rates in the upper part of the stem. Apparently moderate damage is associated with a period of increasing radial growth of the stem in the crown of the tree, where damage is most prevalent (Fig. 14). The larger rings often consist of "redwood" (Fig. 21). Later, when damage becomes severe with branch dieback and most buds inhibited, the growth rate drops markedly, especially in the middle and upper crown regions. This decreased growth rate is probably the cause of the decreased volume content of trees in the severe and aphid-killed damage classes (Balch 1952; Warren, Parrott and Cochran 1967; and Schooley 1976a). Radial growth patterns at breast height are probably similar, but of a lesser magnitude than those in the middle and crown regions.

A combination of local height/diameter curves for fir from several parts of the Island with the special volume tables for aphid damaged trees from western Newfoundland shows estimates of individual tree merchantable volumes ranging from an increase of 23 percent for moderately damaged trees to a loss of up to 15 percent for severely damaged trees, as compared to undamaged trees of the same breast height diameter (Page 1975).

Shortened and missing leaders and main stem branches alter crown shape and volume of trees. Trees in the severe damage class usually have crowns shaped like cone frustrums rather than like the typical cone shaped crowns of undamaged, lightly damaged and moderately damaged trees (Fig. 22) (Schooley and Oldford 1974b). Crown volume is 25 to 30 percent less in the light, light-to-moderate and moderate damage classes as compared to undamaged trees; it decreases by as much as 80 percent or more in severely damaged trees. This reduces the photosynthetic surface and must contribute significantly to the overall reduction in growth rate of severely damaged trees.

Susceptibility to Further Damage from Other Organisms

Infestation by the balsam woolly aphid alters the normal physiological processes of balsam fir and as a consequence resistance to further damage by disease organisms or other insect species is also changed.

There is a relation between the level of aphid damage and the incidence and intensity of Armillaria root rot caused by *Armillaria mellea* (Vahl ex Fr.) Kummer (Hudak and Wells 1974). Studies show that the root rot affects undamaged as well as aphid-damaged trees but the

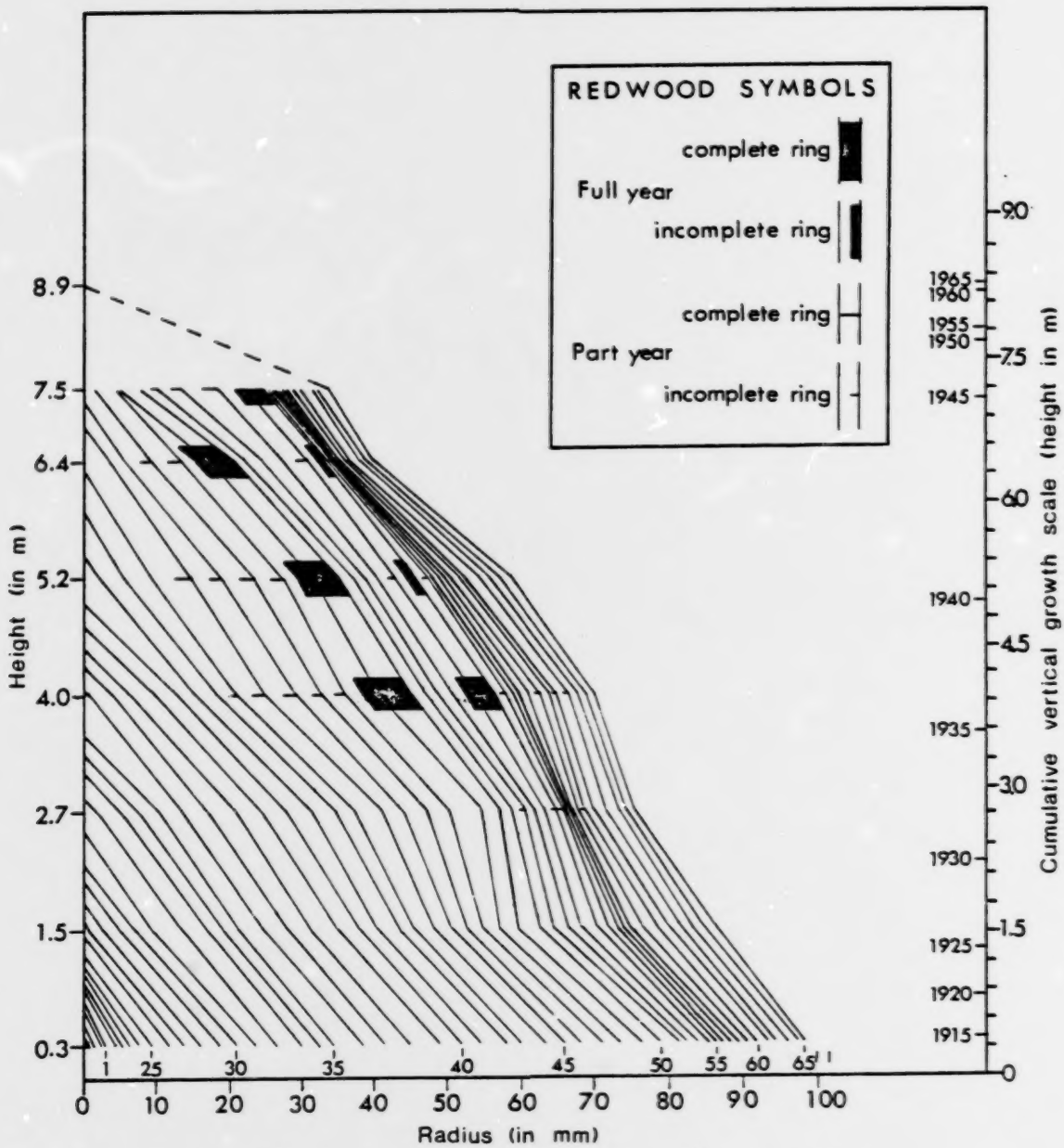

Fig. 21: Radial increments at 1.2 m intervals, vertical growth in 5-year intervals and redwood pattern (Warren et. al. 1967).

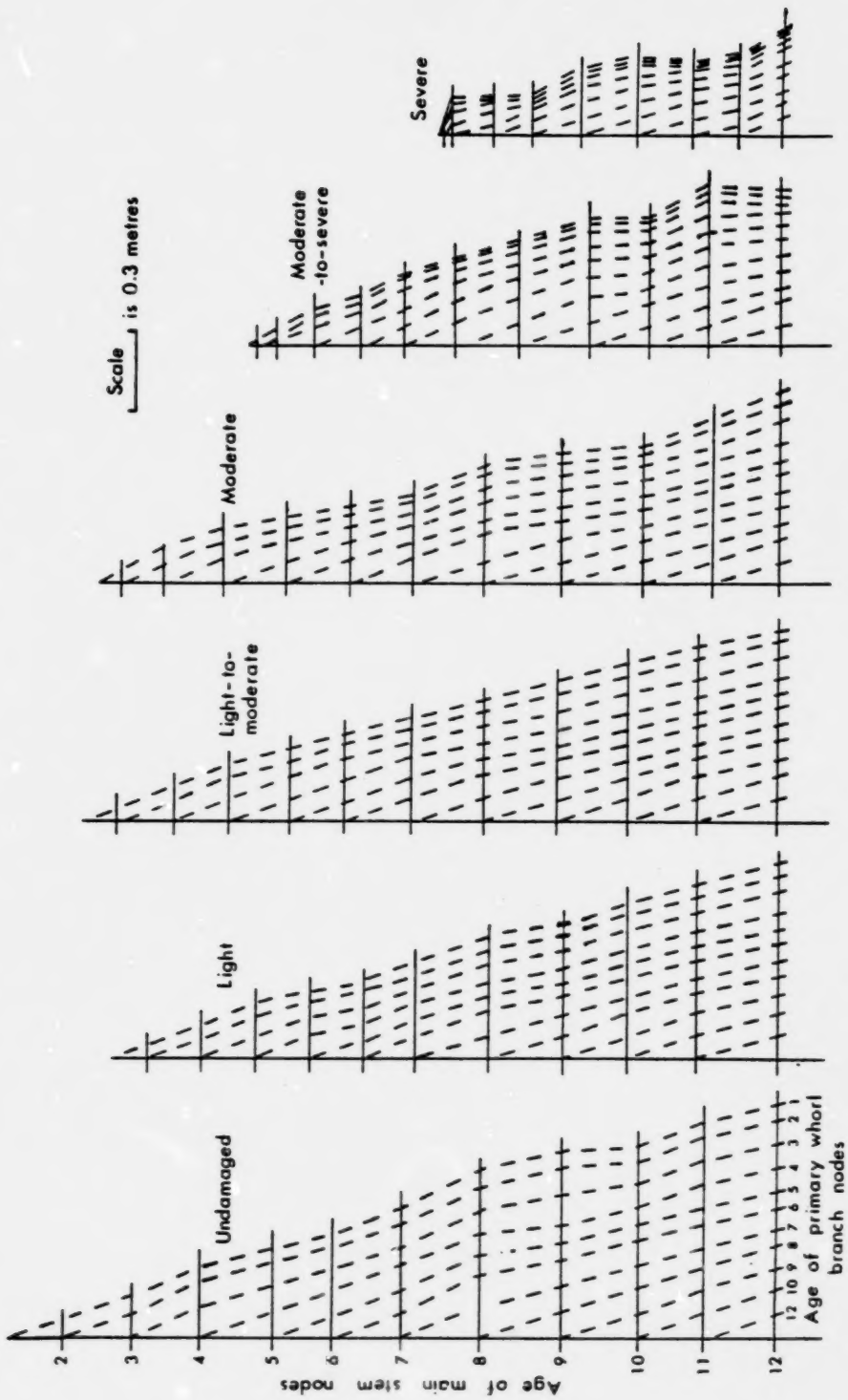

Fig. 22. Annual elongation of the main stem and primary whorl branches in the upper 12 years of balsam fir trees in 6 classes of aphid damage. (Schooley and Oldford 1974b)

incidence of the disease, expressed as the percentage of infected trees, increases with the level of damage regardless of site quality (Table 4). In addition, the percentage of infected roots, the length of mycelial fans on infected roots and the average percentage of root circumference covered by mycelium increases as aphid damage increases from light to severe. These data indicate that aphid damage is a primary factor predisposing trees to infection by *A. mellea*. This fungus destroys the cambium and phloem of roots and root collar and reduces the concentration of most macro-nutrients (Singh and Bhure 1974). The high proportion of root length and circumference covered by mycelial fans indicate that *A. mellea* is an important factor contributing to the mortality of trees severely damaged by the aphid. The fungus is common in most forest soils in Newfoundland and stands with the most aphid damage are expected to have the highest percentage of infected trees.

Table 4.- Incidence and intensity of Armillaria root rot in balsam fir in five aphid damage classes.

Damage class	No. trees examined	Percent trees infected	No. roots examined	Percent roots infected	Extent (%) of mycelial fan along root	Extent (%) of mycelial fan around root
Undamaged	40	2.5	120	0.8	11.1	8.0
Light	50	4.0	150	2.0	26.8	10.0
Moderate	50	20.0	150	7.3	36.3	39.0
Severe	50	32.0	150	14.6	63.7	80.0
Dead	50	88.0	150	69.6	77.3	90.0

Davidson and Etheridge (1963) show that *Stereum sanguinolentum* (Alb. & Schw. ex Fr.) Fr., the organism causing most of the heart rot in balsam fir infects the tree through wounds on living stems and branches. Attempts to isolate this fungus from aphid-damaged branches did not yield a single culture and it is concluded that aphid damage has no direct relationship with the incidence of the heart rot organism (Hudak 1975).

Weakened trees are often attacked by bark beetles, wood wasps and other wood boring insects. The role of these insects in the decadence and mortality of balsam fir damaged by the balsam woolly aphid has not been investigated in detail. However, it is reported (Stillwell 1966; Basham et al 1974) that wood wasps oviposit in balsam fir trees weakened by spruce budworm and balsam woolly aphid attack and simultaneously

introduce their fungal symbiont, *Stereum chailletii* (Pers. ex Fr.), into the xylem of host trees. Consequently, this fungus is well established in the sapwood before tree mortality occurs. Hudak (1975) reports that *S. chailletii* does not occur in the xylem until the trees accumulate severe aphid damage. Three species of wood wasps, *Sirex cyaneus* F., *S. juvencus* (L.) and *Urocerus albicornis* F., were collected from bolts of aphid-damaged trees and as many as 50 oviposition holes were counted on a 30 cm long stem section. It is evident that the wood wasp *S. chailletii* association is an important factor culminating in tree mortality.

The effects of aphid damage on the initial development of outbreaks of defoliating insects such as spruce budworm, *Choristoneura fumiferana* (Clem.), and hemlock looper, *Lambdina fiscellaria fiscellaria* (Guen.), are not known. However, defoliation by these insects is more detrimental to the survival of trees as the level of aphid damage increases (Otvos et al 1971).

Trees that have been damaged by the aphid are also more susceptible than healthy trees to top breakage caused by ice accumulation or wind. Top breakage is most common on trees that have recovered from aphid damage. The new crown growth that develops above the damaged part of the trees often breaks off because it is abnormally exposed above the stand canopy.

Wood Properties and Utilization

The physical and chemical properties of redwood or abnormal xylem produced as a result of aphid attack are different from those of normal wood and its presence is detrimental to most forms of wood utilization. Dyer and Thaxter (1957), Hunt (1968) and de Montmorency (1966) report a lower amount and inferior quality pulp from aphid damaged trees. The wood from damaged trees is also undesirable for lumber (Balch 1952).

Average moisture content of undamaged trees decreases from 147% in the top to 128% in the butt section (Hudak 1975). Along the radii of trees, the outer wood is wettest averaging 209%, the inner wood is the driest at 87% and the pith region has intermediate moisture content. Generally, similar distribution of moisture is reported for balsam fir by Etheridge and Morin (1962) and by Clark and Gibbs (1957). This pattern of moisture content is present in living aphid damaged trees but the average values per tree decreases gradually from 133% to 100% as the level of damage increases. The average moisture content in aphid-killed trees decreases abruptly at first, then it gradually levels off between 40% and 50% in trees dead for more than three years. Moisture loss is largest in the upper sections of the bole, especially in the outer portions of radii and it is associated with the occurrence of

advanced saprot. The low moisture content of 40% to 50% in dead trees is not a limiting factor for the growth of microorganisms in wood, and it has no detrimental effect on the mechanical pulping of wood (de Montmorency 1964).

Wood with an unusually high density is formed as a result of balsam woolly aphid attack (Dyer and Thaxter 1957). However, the density of wood samples that do not include redwood do not vary with increasing levels of aphid damage (Hudak 1975). The average density of this wood is 0.342 g/cm^3. Density decreases from the lower sections to the upper sections of the bole and a small and inconsistent variation occurs along the radii. Hale and Prince (1940) report similar changes in density along the length of the bole but also show a decrease from the sapwood to the pith. Hudak (1975) indicates that his sample trees were in the 15 cm and smaller diameter classes and density changes may become more apparent on larger trees.

The density of wood, including aphid caused redwood, in damaged trees increases by 2% to 5% in comparison to undamaged trees (Hudak 1975). This range of increase is interpreted as an approximation of the impact of redwood on the average density of trees. The largest differences, 10.0% to 26.7% occur in the outer wood of the top sections of damaged trees where redwood is most common. The density of wood in aphid killed trees does not decrease by more than 2.0% in comparison with living damaged trees until 4 years after death whether the comparison includes redwood data or not. However, the density, including redwood, decreases by 2.6%, 6.4% and 7.0% in the fourth, fifth and sixth years respectively. These decreases are interpreted as the impact of deterioration by microorganisms on the density of wood. Although most of the reduction is attributable to the decrease in the outer portion and especially in that of the top sections of boles, the density of the inner wood also decreases.

In undamaged trees the average pH was 6.3 and does not vary appreciably along the radii or with increasing heights in the trees (Hudak 1975). Small decreases in pH occur as damage increases and further decreases occur after the trees died. The average pH of severely damaged trees is 5.9 and for trees dead 6 years it is 5.5.

Studies indicate that the amount of lignin occurring in the wood from aphid damaged trees is greater than from undamaged trees. Normal wood formed prior to aphid attack contained 28.5% lignin, while abnormal redwood formed later on the same trees contained 35.0% (Perem 1965). Sulphite wood pulp which is used to make paper is progressively less delignified as the proportion of redwood increases.

The extractives, holocellulose and alpha-cellulose contents of the outer wood of undamaged trees average 2.8%, 72.4% and 40.2% respectively (Hudak 1975). Data of similar magnitude are reported for balsam fir by Clermont and Schwartz (1951) and by Timell (1957). The percentages of these constituents do not vary appreciably with the level of aphid damage except in samples containing redwood that yield a lower amount of holocellulose and correspondingly more lignin. The percentage of these chemical constituents in dead trees remain relatively unchanged for 5 years. Then the extractives content of the outer wood increases to 5.7% and the holocellulose content decreases to 67.5%. However, the alpha-cellulose content remains at 40.8%, similar to that in living damaged trees.

The constant alpha-cellulose content in trees dead up to 5 years is remarkable and has important practical significance. Alpha-cellulose content is the most important chemical factor affecting the yield and quality of chemical pulp (van Buijtenen 1969). Therefore, using trees dead for up to 5 years for manufacturing chemical pulp should have no detrimental effect on the quality of the product, and the yield on the weight basis also should not decrease greatly. However, on the volume basis the yield would be reduced as signified by the approximately 6.7% decrease in the density of the wood. Additional yield losses may be caused by debarking and other mechanical preparations of wood prior to pulping.

The mechanical properties of redwood are similar to compression wood (Perem 1965). Compression wood has generally low tensile strength parallel to grain, low stiffness and on the basis of comparison it is thought that redwood has similar weaknesses. Differences in the amount of longitudinal shrinkage between normal wood and redwood can cause the development of considerable stresses when a piece of lumber is dried or when it is resawn after drying. These stresses result in twisting and warping. The proportion of redwood present in lumber determines how the lumber may be utilized.

Deterioration

Hudak (1975) shows that the sapwood in merchantable stems of living balsam fir trees damaged by the aphid up to the moderate level is free from deterioration by decay organisms. Bio-deterioration commences in severely damaged trees but advanced saprot, reducing the hardness of the wood does not occur until the third year after death. The progress of radial penetration by both incipient and advanced saprot in trees killed by the aphid is shown in Fig. 23. Incipient rot penetration is deepest in the butt section of trees and shallowest in the top while advanced saprot penetration is deepest in the top sections and least at breast height. Similar investigations by

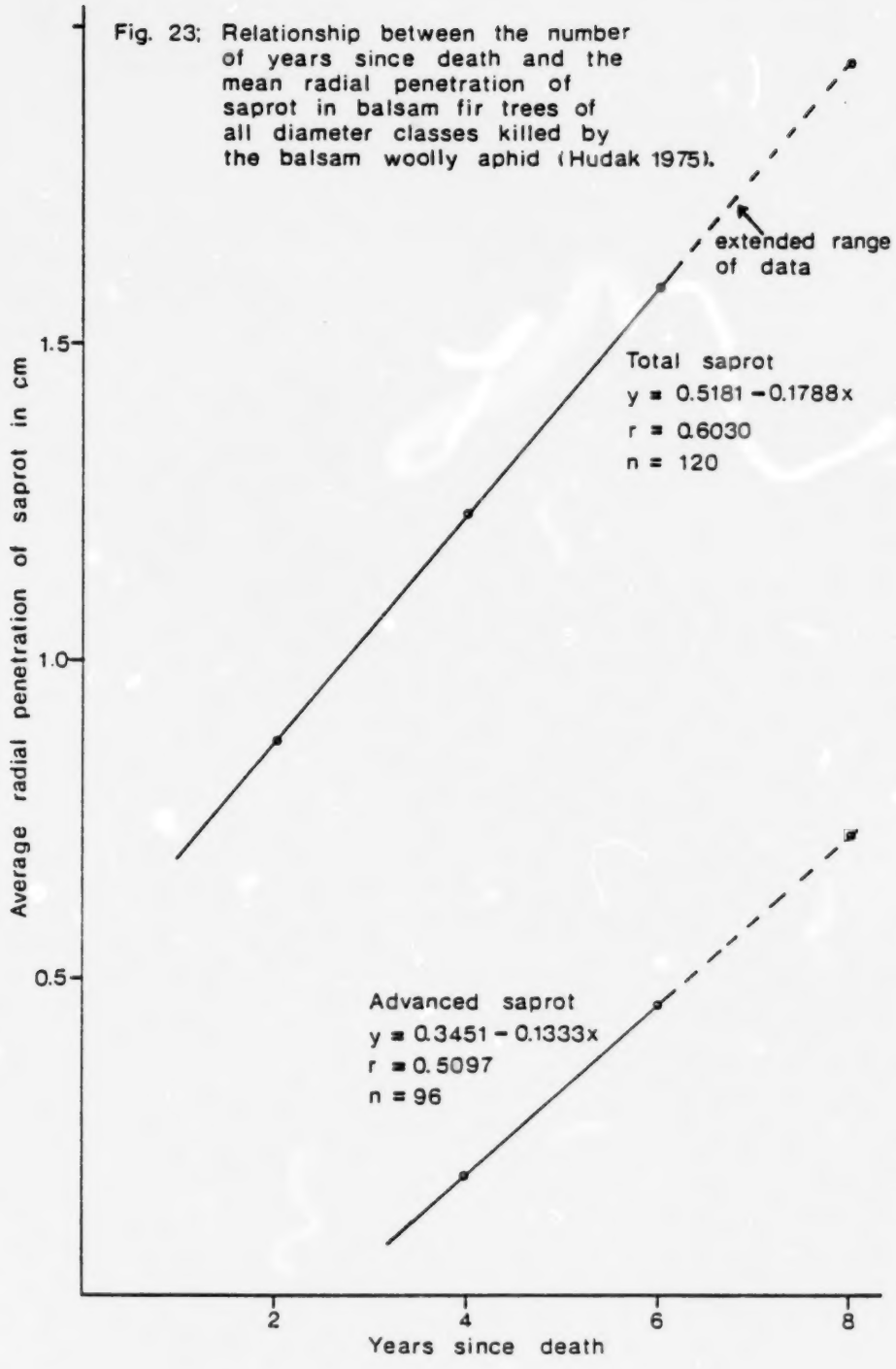

Fig. 23: Relationship between the number of years since death and the mean radial penetration of saprot in balsam fir trees of all diameter classes killed by the balsam woolly aphid (Hudak 1975).

Basham (1959) in Ontario, by Stillwell and Kelly (1964) in New Brunswick and by Basham et al (1974) in Eastern Canada show that the progress of both incipient and advanced rot penetration in fir trees killed by the spruce budworm is faster than it is in trees killed by the aphid in Newfoundland.

Bacteria and at least 58 species of fungi occur in the stems of fir in Newfoundland (Hudak 1975). The bacteria are largely confined to the pith region. The five most frequently occurring fungi, in decreasing order of occurrence, are *Stereum chailettii*, *Kirschteinella thujina*, *Polyporus abietinus*, *Rhinocladiella atrovirens* and a *Cephalosporium* sp. They comprise more than 50% of all fungi. The succession of organisms associated with saprot begins with the reddish-brown staining fungi *S. chailletii* which is frequently introduced by wood wasps into severely damaged trees. Later it is followed by blue-stain fungi such as *K. thujina*, *R. atrovirens* and *Phialophora* species and finally by *P. abietinus*, the climax species, a white pocket rot which causes most of the advanced saprot. The succession of organisms in the outer wood is more or less repeated, with a time lag, in the heart wood and pith. Both *S. chailletii* and *P. abietinus* occur first in the sap wood and later both species also occur in the heart wood and pith.

A. mellea is among the less frequently occurring fungi in the stems of balsam fir killed by the aphid (Hudak 1975). This appears to contradict an early report that the incidence and severity of Armillaria root rot increases with the level of aphid damage (Hudak and Wells 1974). However, in the earlier report the incidence of the root rot is based on the percentage of infected trees. Many of the lowermost sections of trees contained the mycelial fans between the bark and xylem but isolation attempts made just beneath the latest annual rings did not yield cultures of *A. mellea*. Such results indicate that *A. mellea* is more important in the mortality of trees damaged by the aphid than in the actual deterioration of the xylem in dead trees.

The role of bacteria, imperfect fungi and Ascomycetes in the deterioration process cannot be ignored. Although the manifestation of their effect on wood properties is much slower than that of the classical decay fungi, numerous reports demonstrated that many species are capable of localized or even extensive degradation of the xylem cell walls. Decaying wood in natural field conditions must be considered as a complex biological community of micro-organisms marked by interaction and succession among the members of the community.

The radial penetration of saprot at breast height approximates the mean of rot penetration along the merchantable bole (Hudak 1975). Based on this relationship, a set of simple linear regressions was developed for estimating the percentage of saprot content of standing trees by diameter classes (Fig. 24). These data indicate the proportion of the trees in which deterioration by microorganisms occurs.

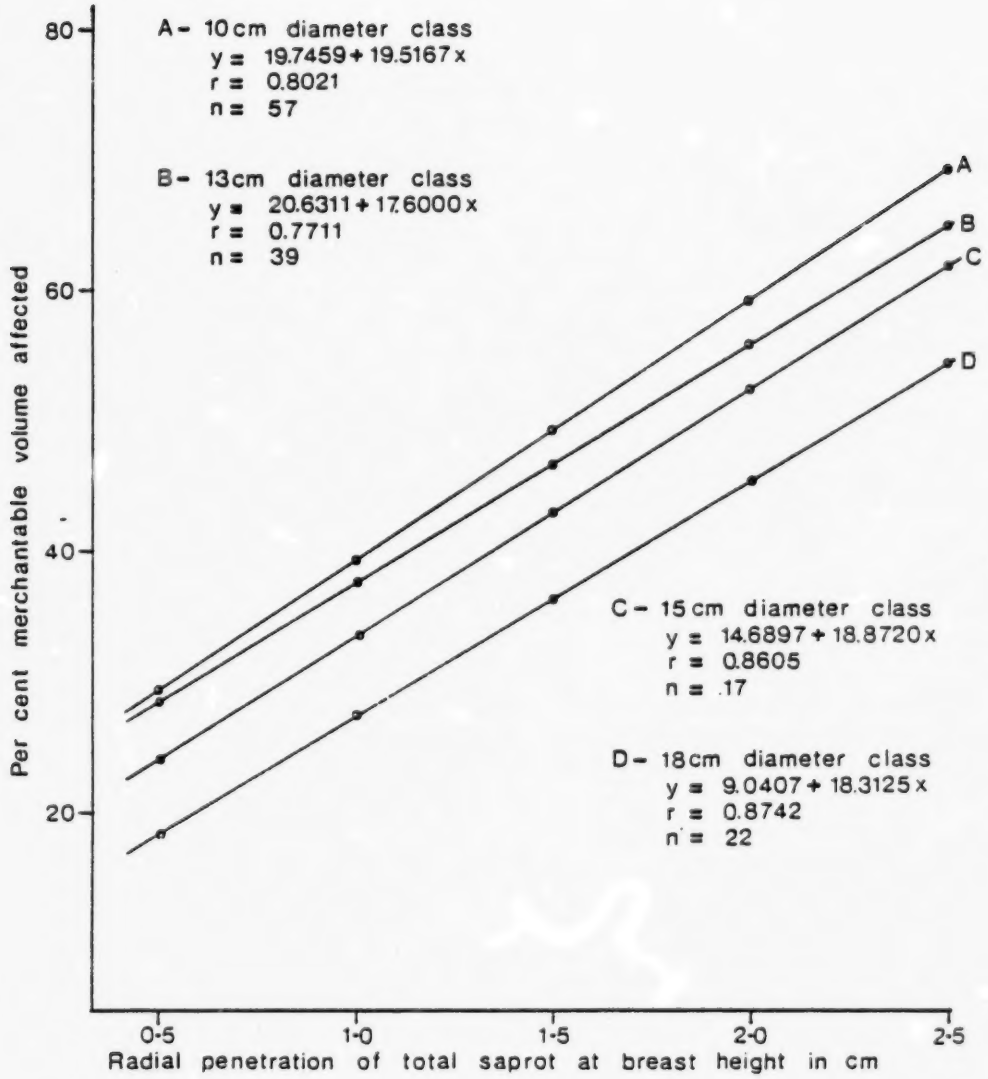

Fig. 24: Relationship between radial peneration of saprot at breast height and the percentage of merchantable volume affected by saprot in dead balsam fir trees of 10 cm, 13 cm, 15 cm and 18 cm or higher diameter classes (Hudak 1975).

Damage and Recovery in Relation to Tree Characteristics

Trees of any height, age or diameter may be damaged by the aphid but generally the ability of trees to withstand or to recover from damage decreases with age. Damage also becomes apparent, and reaches a severe level most rapidly, on taller, older and dominant trees. Data from semi-mature and mature stands, where all levels of aphid damage were present showed that the average age, height, diameter and crown class rating for trees in each of the various damage classes were larger as the severity of damage increased (Table 5)(Page 1973). In one stand for example, the average severely damaged tree was almost 6 m taller, 15 years older and 8 cm larger in diameter than the average undamaged tree. This same trend was observed among young trees. These relationships suggest that good tree growth promotes the successful development of aphid populations or the development of symptoms of aphid damage. However, when an aphid outbreak becomes well established in an area, the relationships tend to disappear because the overall level of damage becomes more severe. Also, the relationships become less apparent if the outbreak subsides and recovery occurs.

Table 5.- Average tree height, age, diameter, and crown classes of balsam fir trees in four aphid damage classes.

Parameter	Aphid damage class[a]			
	U	L	M	S
Average height (m)	6.1	6.2	7.6	8.1
Average breast height age (years)	37.3	40.7	44.3	46.8
Average DBH (cm)	7.9	8.6	10.9	11.7
Average crown class rating[b]	2.1	2.1	2.5	2.4

[a]Based on plots having all aphid damage classes evaluated by average condition in the upper and lower crown halves.

[b]Derived by summation, using ratings of 1 for suppressed stems, 2 for intermediate stems, 3 for co-dominant stems, and 4 for dominant stems.

The degree of recovery among trees repeatedly damaged by the balsam woolly aphid is as yet unknown but it is quite possible that this may be an important factor for the continuation of balsam fir as a merchantable species in areas susceptible to infestation. Immature

trees may withstand severe attack for several years during several periods of infestation and recover each time to a reasonably vigorous condition (Fig. 25). This has happened frequently, and there is now less concern over the effect of aphid attack on young tree development than was expressed in the past. Mature and overmature trees are less able to show this response than are younger trees (Warren, Parrott and Cochran 1967). Their deterioration may continue even though the infestation has subsided.

THE EFFECTS ON FOREST STANDS

Regeneration and Young Stand Development

Stands of fir regenerate themselves whether the original stands were affected by the balsam woolly aphid or not (Fig. 26). This occurs because the production of seed for replacement trees and natural succession are usually not seriously affected by aphid attack (Schooley 1975, 1976b; Hall and Richardson 1973). However, regeneration surveys show that stands as young as six years of age at the stump are attacked by the aphid (Schooley and Oldford 1974a). Damaged trees occurred in 20 of 23 stands examined; five stands had 1-10% of fir trees damaged, ten stands had 11-50% damaged and the remaining stands had more than 50% of trees damaged. Ten of the stands had some severely damaged trees. In these stands the damage to individual trees was more severe where more trees were damaged. About half of all damaged trees recorded were in the light or light-to-moderate damage classes and a further one-third had recovered.

Survey results also show that aphid attack caused tree mortality in only four of the 23 stands. Mortality averaged only 0.5% in three stands that were 18 years old or less at the stump. In the other, a 30-year-old stand, about 5% of the trees were killed by the combined effects of aphid damage and suppression. The low incidence of mortality may be unfortunate because stand densities averaged 67 000 stems per hectare and would benefit from thinning (Schooley and Oldford 1974a).

These survey results indicate that most young fir stands have not been seriously affected by the aphid but data also show that recovered trees are not immune to renewed attack. Therefore, future losses will probably become significant if the aphid infestation persists and damage occurs repeatedly over the life of the stands. Study of the long term effects of repeated aphid attack beginning at an early stand age is the focal point of current aphid research in Newfoundland.

Semi-mature, Mature and Overmature Stands

In semi-mature stands individual severely-damaged trees often show significant decreases in height and radial growth, but the proportion of such trees in a stand at any one time is usually small. Other less

Fig. 25: Recovery from aphid damage in a semi-mature balsam fir stand.

Fig. 26: Balsam fir regeneration beneath the remnants of parent stand killed by the aphid.

severely-damaged trees, under reduced competition, may increase growth to occupy the additional growing space. Consequently, the net effect of aphid attack on semi-mature stands is generally low if not negligible. The greatest effects of aphid attack occur in overmature stands, where a high proportion of the trees are severely affected or killed and insufficient healthy trees are left to occupy the available growing space (Warren, Parrott and Cochran 1967).

The height/diameter relation in damaged semi-mature stands is usually similar to that in undamaged stands because of the compensating effects described above. Height reductions of up to 1.5 m are recorded in a few areas of insular Newfoundland, but again only where severe levels of damage occur (Page 1973). In the majority of mature stands, height differences between damaged and undamaged trees are very small or non-existent (Page 1975).

The number of stems per hectare in relation to the average diameter breast height and average age in damaged and undamaged stands measures the degree to which aphid attack affects site occupancy and the normal rate of stand development. No reduction in site occupancy or in the rate of stand development is apparent in data from 24 locations sampled in insular Newfoundland (Page 1973, 1975, 1976; Bryant 1976).

To obtain estimates of merchantable volume loss resulting from aphid damage, local height-diameter curves and special volume tables for aphid-damaged trees were used to calculate both the standing volume and the expected undamaged volume in each of 424 sample plots (Page, Schooley and Hudak 1970; Page 1975; Bryant 1976). The difference between the standing volume and undamaged equivalent volume was assumed to be the change in merchantable volume caused by aphid attack. The results show that the average loss should not exceed 4 percent in the living component of plots. These values are, respectively, the lower and upper limits of 95% confidence bands of the estimated volume changes on 56 and 72 plots in each of two areas affected by aphid attack (Table 6). In 22 other areas sampled less intensively, estimated volume changes are within these limits.

The above estimates of losses relate only to the merchantable volume of living trees in aphid-affected stands. Trees killed by aphid attack were measured in 290 sample plots and their total volume was 4.5 percent of the existing merchantable volume (Table 7). The volume of dead trees in selected plots was much higher, amounting to 20.3% of the existing volume. Such high losses are observed in severely damaged overmature stands (Warren, Parrott and Cochran 1967). However, it should be remembered that trees killed by the balsam woolly aphid do not represent an immediate loss of stand volume (Hudak 1975). The physical and chemical properties of the wood of dead trees remain suitable for manufacturing wood pulp for a period of about 4 to 5 years.

Table 6.- Estimates of merchantable volume (m^3) for living trees in aphid-damaged sample plots and volume losses and increases associated with aphid damage (Adapted from Page 1975 and Bryant 1976).

Data set	No. of plots	Balsam fir only			All tree species		
		Average volume	% vol. change	SE (%)	Average volume	% vol. change	SE (%)
Area 1	61	106.0	-0.57	0.08	162.6	-0.37	0.05
Area 2	56	175.1	+6.28	0.01	210.0	+5.24	0.01
Area 3	72	179.8	-3.45	0.08	285.9	-2.17	0.05
9 areas[a]	18	51.5	-0.67	<1.95	62.6	-0.54	<1.68
13 areas	83	301.5	<-6.15[b]	<0.43	429.3	<-4.14[b]	<0.29

[a]Selected aphid-damaged forested areas.

[b]Value not amended per Bryant 1976.

Table 7.- Merchantable volume of balsam fir trees killed by aphid attack and proportion of killed volume to merchantable volume of all living trees in aphid-affected sample plots.

Data set	No. plots	Average vol. (m^3)	Aphid-killed trees	
			vol. (m^3)	% of existing
Area 1	61	162.6	4.6	2.8
Area 2	56	210.0	0.9	0.4
Area 3	72	285.9	5.5	1.9
13 areas	83	429.3	28.3	6.6
9 areas[a]	18	62.6	12.7	20.3

[a]Selected aphid-damaged forested areas.

Therefore, high volume losses would most probably occur in stands where extensive tree mortality developed over a short period of time and harvesting was not possible before substantial deterioration occurred.

Damage in Relation to Site and Stand Characteristics

Elevation In Newfoundland there is a strong positive relation between elevation and the occurrence and severity of damage (Page 1973, 1975). Similar relations with damage are recorded for grand fir and amabilis fir in Washington (Johnson, Mitchell and Wright 1963) and British Columbia (Carrow 1973). In Newfoundland, analysis of the variety of conditions indicates that damage virtually always appears first at or near the lowest elevation in a given area and that it continues to develop at increasing altitudes for at least 15 years. However, the rate of spread to higher elevations seems to decrease with time, and the maximum elevation of damage tends to increase with increasing age of the stands, at least to about 45 years age at breast height (50 to 60 years total age). The elevation at which this apparent equilibrium is reached is affected by the height of the surrounding hills. Under equilibrium conditions, damage reaches the tops of hills up to about 130 m or 150 m in elevation, but ceases about 100 m below the top of 330 m hills and 270 m to 300 m below the top of 700 m hills (Fig. 27). Severe damage usually ceases at 15 m to 100 m below the maximum elevation for all damage. These data suggest that any equilibrium that is attained is essentially climatic in origin.

Soil and Topographic Characteristics Damage is more prevalent and more severe in stands growing on dry and fresh sites than in those on moist and wet sites (Page 1975; Fig. 28). Similar differences exist between stands on freely drained soils (podzols, brunisols and lithosols) and those on poorly drained soils (gleysols and organics). More severe damage also tends to be associated with steep slopes, rocky knolls, and sites with shallow humus layers and relatively coarse-textured soils, but patterns are generally less well-marked and less consistent than those for moisture regime and soil order. No meaningful association between aspect and the incidence and severity of damage has been recorded in Newfoundland.

All these relations are believed to be direct or indirect indicators of an association between moisture stress and aphid damage. Site conditions that are most commonly associated with the presence of severe aphid damage are all conducive to the development of moisture stress periodically during the growing season. The interference with normal water transport that occurs as a result of aphid attack (Puritch 1971, 1973) is thus much more pronounced on the sites where water stresses already exist, leading to the more rapid development of severe damage.

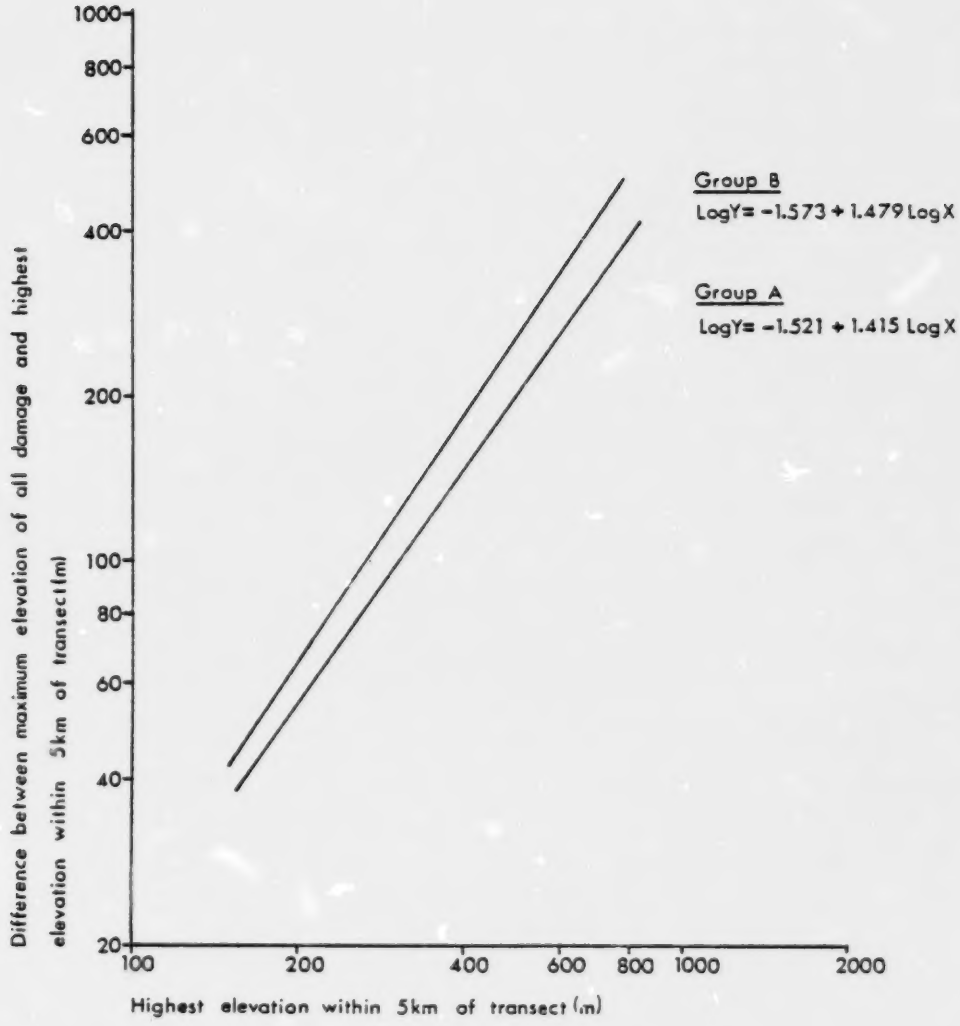

Fig. 27. Differences between the maximum elevation of all aphid damage (Group A) and of severe damage (Group B) and the highest elevation within 5 km of transect, in relation to the height of sheltering hills.

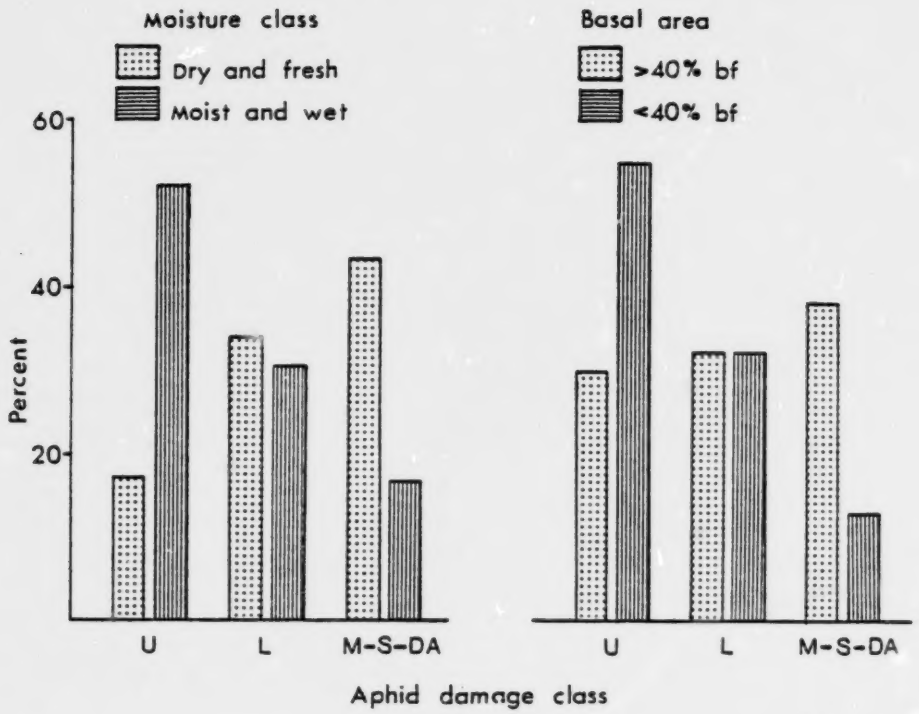

Fig. 28; Distribution of balsam fir trees among aphid damage classes for plots sorted by moisture classes and by portion of balsam fir content. (U-undamaged, L-light, M-moderate, S-severe and DA-dead).

Stand Characteristics Greater stand dominant heights are associated with more severe levels of damage, though in many cases differences are not very large (Page 1975). Again it appears that the taller stands, which are normally under greater stress because of their greater transpiration requirements and the greater heights to which water must be lifted, are the ones most seriously affected when aphid attack further increases the difficulties of water transport. A somewhat similar association between site quality (as measured by site index and by vegetative community) and aphid damage is reported by Johnson, Mitchell and Wright (1963) from Washington.

Increasing age is usually well correlated with increasing height and diameter, and hence with increased moisture stress. Frequently, the larger, older stands are the ones most severely affected by aphid damage, and it was in stands of this type that most of the severe damage that developed in the western part of the Island during the 1950's was located (Warren, Parrott and Cochran 1967). Many of these stands have now been destroyed as a result of damage by the aphid and other pests such as the eastern hemlock looper and the spruce budworm.

The proportion of balsam fir in infested stands is also related to the severity of aphid damage. Stands composed of more than 40% fir by basal area have been found to have up to 6 times as many stems in the moderate, severe and dead damage classes as stands composed of less than 40% fir (Page 1975; Fig. 28). It is probably that this relation is, at least partly, an indirect reflection of the same site moisture/damage relations already discussed, in that many of the stands composed mostly of balsam fir occur on the drier, freely drained sites, especially in western Newfoundland. A similar, somewhat complementary, relation also exists between damage accumulation and total balsam fir basal area. Damage reaches more severe levels where balsam fir basal area exceeds about 23 m^2 per hectare, that is a stand in which the main component is fir and which usually occurs on productive, freely-drained sites. However, it is also possible that both the proportion and the absolute amount of balsam fir in a stand may directly affect the spread and build-up of aphid populations and hence the amount of damage that accumulates.

Under undisturbed conditions there does not appear to be any direct association between stand density and aphid damage. Nor is there any quantitative evidence from Newfoundland to support earlier evidence from the Maritime Provinces (Balch 1952) that damage is more severe on open-growing trees and along stand margins. Damage may, however, increase if semi-mature or mature stands are thinned, but this is probably a result of the disturbance to the growing site rather than of the change in density itself.

DAMAGE HAZARD RATING SYSTEM

A damage hazard rating system, based on the site and stand parameters found to be associated with variations in the incidence and severity of aphid damage, has been developed in Newfoundland (Page 1975). The system consists of two parts: the first defines the overall risks of damage in terms of three elevation classes and the second defines gradations of hazard under four site and stand conditions.

The three elevation classes are (I) lands below maximum elevations for occurrence of severe damage and tree mortality, (II) lands above the preceding but below the maximum elevation of any class of damage, and (III) lands above the preceding and in which there is a low probability of any aphid damage and no hazard of severe damage (Fig. 27; Page 1975).

Approximately 40% of Newfoundland, except the Northern Peninsula north of Bonne Bay, occurs in elevation classes I and II and therefore may contain balsam fir stands at risk. Of the 4.5 million hectares in these classes at risk, 3.2 million hectares are in elevation class I of which 2.5 million hectares are productive forest sites and the remainder is unproductive or non-forest area. In elevation class II 0.5 million hectares are productive forest sites and 0.8 million hectares are non-forest.

Within elevation classes I and II, stands are assorted in relation to four parameters: soil moisture regime, percent balsam fir by basal area, total basal area of balsam fir, and stand breast-height age (Fig. 28; Page 1975). These parameters were selected on the basis of their relatively consistent and significant association with variations in aphid damage and their relative ease of determination. The risk for stands is based on the proportion of severely damaged and killed balsam fir, calculated by basal area (Page 1975; Table 8).

The application of the hazard rating system is illustrated in Fig. 29 which shows a portion of the Crabbes River drainage and in Fig. 30 which shows portions of the Deer Lake and Glide Lake drainages. In these examples, stands about 180 m elevation are not at risk to severe damage and tree mortality during or after an aphid outbreak. The stands in the highest hazard category, i.e. over 30% of stand basal area aphid-killed or severely damaged are contained within the shaded area. These areas were identified by the prevalence of fir and using height class as an indication of age (from data provided by the 1968 Forest Inventory). To specifically identify stands in the high hazard class, on-site inspection is required to determine which stands are on dry-fresh sites and contain over 9 m^2 of balsam fir basal area.

Table 8.- Expected proportion (basal area basis) of balsam fir in the severe and dead classes in elevation class I and II stands identified by breast height age, proportion and total content of balsam fir, and moisture regime (Page 1975).

Moisture regime	Percent balsam fir by basal area	Total balsam fir basal area (m^2)	Breast height age classes (years)		
			< 25	25 - 45	< 45
			Expected % basal area damaged		
ELEVATION CLASS I					
Dry-fresh	< 40	Any value	6-11	12-17	24-29
	< 40	< 9	18-23	24-29	30+
		< 9	18-23	30+	30+
Moist-wet	< 40	Any value	1-5	1-5	12-17
	> 40	< 9	1-5	18-23	18-23
		> 9	6-11	24-29	24-29
ELEVATION CLASS II					
Dry-fresh	< 40	Any value	0	1-5	12-17
	> 40	< 9	6-11	12-17	18-23
		> 9	6-11	18-23	18-23
Moist-wet	< 40	Any value	0	0	1-5
	> 40	< 9	0	6-11	6-11
		> 9	0	12-17	12-17

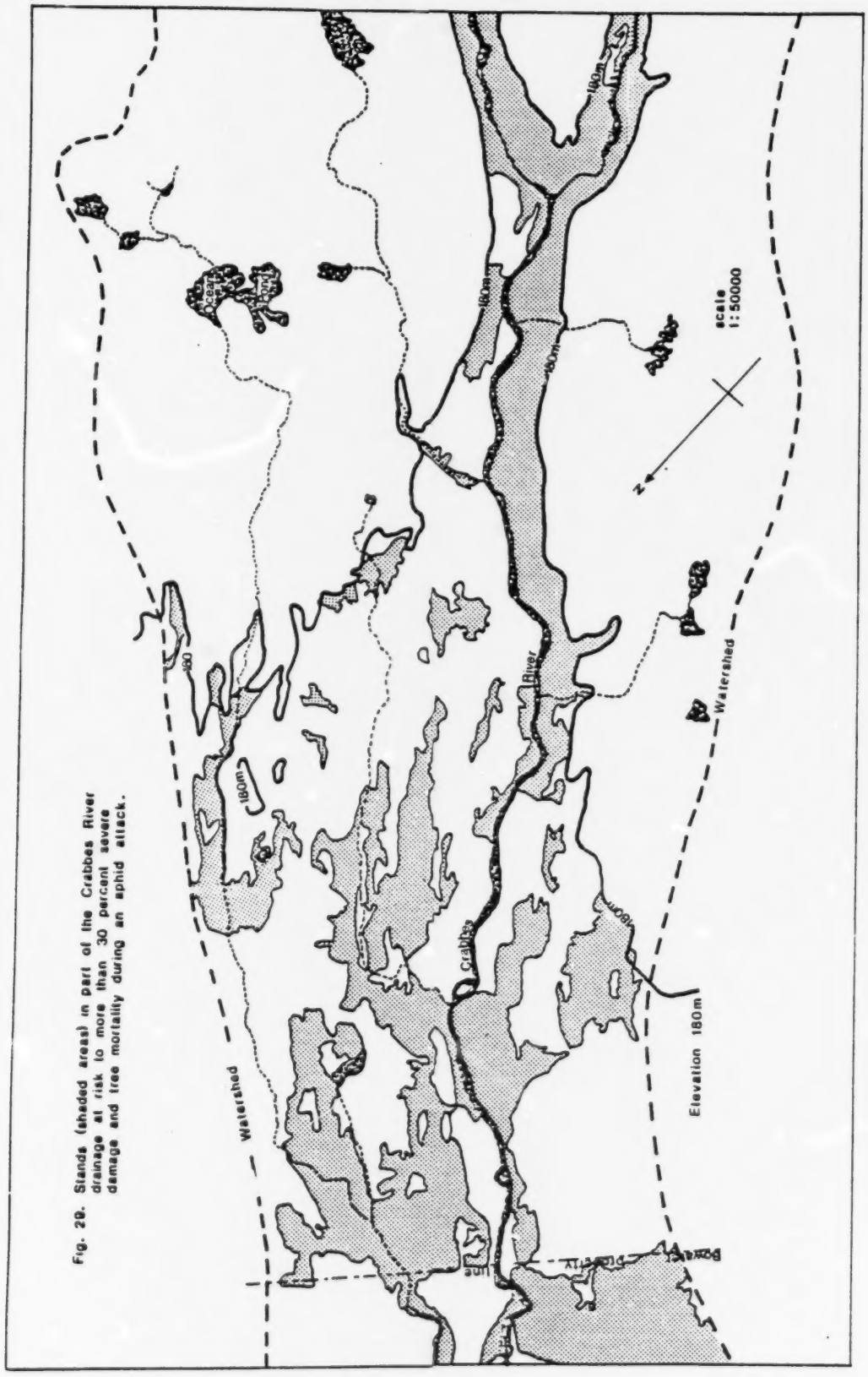

Fig. 28. Stands (shaded areas) in part of the Crabbes River drainage at risk to more than 30 percent severe damage and tree mortality during an aphid attack.

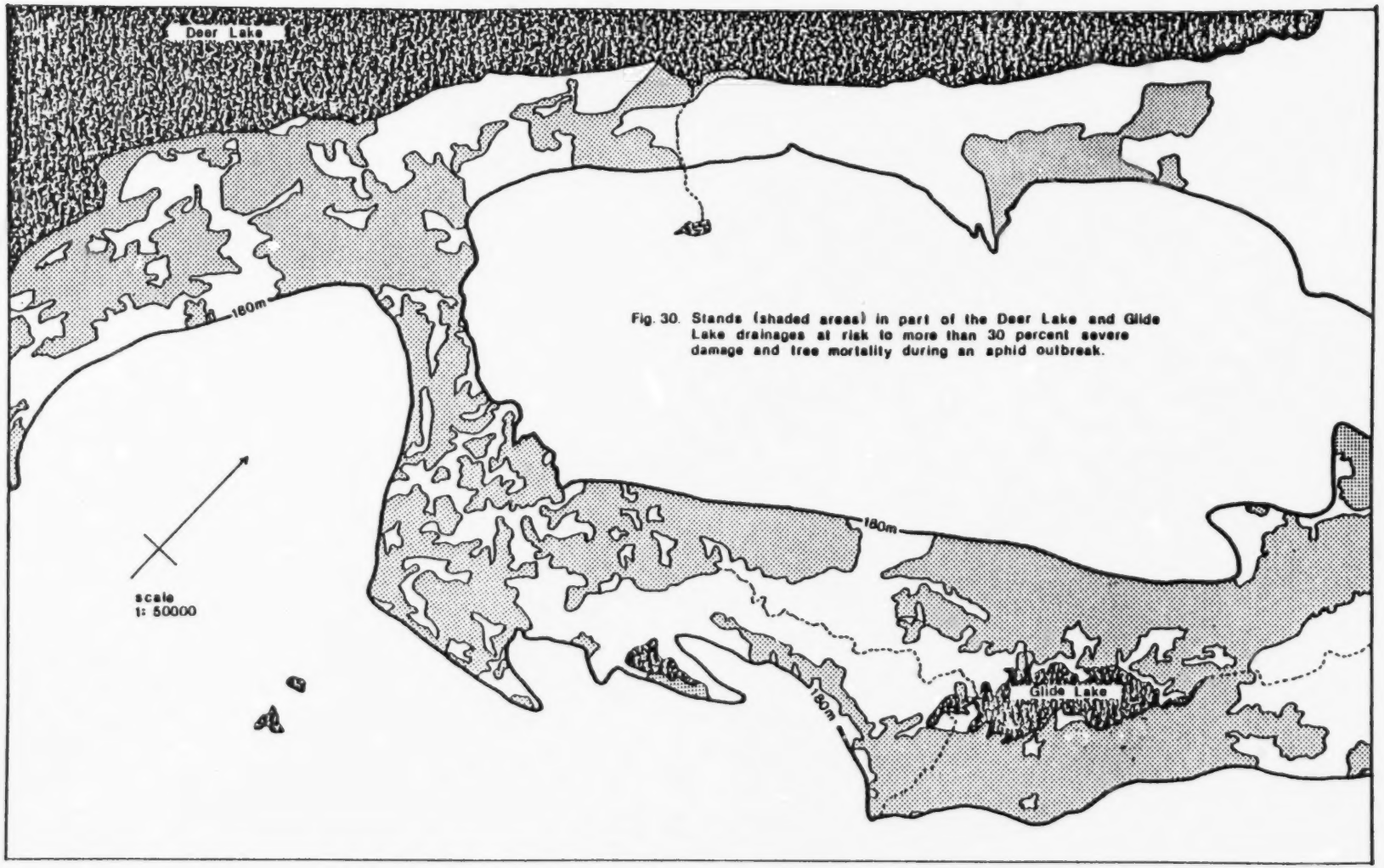

Fig. 30. Stands (shaded areas) in part of the Deer Lake and Glide Lake drainages at risk to more than 30 percent severe damage and tree mortality during an aphid outbreak.

METHODS APPLIED TO CONTROL THE APHID

Natural factors limiting aphid populations, i.e. climate, weather, host tree reactions, and the viability of the aphid have already been discussed. Besides these control factors, several biological, chemical and silvicultural methods have been applied (Bryant 1974b). However, these methods are only effective for small high value stands or individual ornamental trees; none have proven technically or economically feasible over large forested areas.

Of the biological control factors, insect predators are the most common and potentially most effective. The aphid has no known parasites; only two disease organisms, which appear to be largely saprophytic, have been recorded in Europe and North America (Smirnoff and Eichhorn 1970; Clark et al 1971). Three native predators, *Leucopis americana* Mill., *Tetraphleps americana* Pars. and *Hemerobius stigmaterus* Finch have been observed to feed on the aphid but are not capable of reducing numbers below the level where injury occurs. The introduction of predacious insects from countries where the aphid occurs naturally was initiated in 1952 (Carroll and Parrott 1959) and continued periodically until 1968. A total of 16 predator species were introduced but only five, *Leucopis* spp., *Aphidoletes thompsoni* Mohn., *Aphidecta obliterata* L., *Laricobius erichsonii* Rosen. and *Cremifania nigrocellulata* Cz. have become established (Clark, Otvos and Pardy 1973). Some of these species became established in the crowns of infested fir only when aphid population levels were high, in excess of 15 aphids per node. However, balsam fir can be severely damaged at population levels of only four aphids per node. Therefore, all indications are that the introduced predators, together with five known native species, have little or no influence in reducing aphid numbers in the crowns of trees to levels which do not cause economically important damage. Similar conclusions have been drawn from studies conducted in New Brunswick and British Columbia and in the states of Maine, Oregon and Washington in the United States (Mitchell 1962, Clark et al 1971). The present predator complex failed to achieve effective control of the aphid for a variety of reasons:

(a) The introduced predators only build-up to effective control levels when aphid populations are moderate or high on the stem or in the crowns of host trees.

(b) The searching ability of predator larvae is limited, particularly among aphids dispersed in the crowns of trees.

(c) There is a definite time lag in predator population build-up in relation to aphid populations which are capable of increasing more rapidly.

Commencing in 1963 and continuing until 1972 more than 30 insecticides were tested. Under laboratory conditions all insecticides were effective when concentrations were excessively high and the trees thoroughly soaked. This extreme treatment was necessary to reach aphids protected under bud scales or in the flower cups on the twigs and branches in the crowns of trees. However, for aerial application over extensive areas, environmental and economic considerations demand the use of low concentrations and low volumes of insecticides. Only four insecticides, the most promising of those examined in the laboratory, were tested in the field under aerial spray conditions. Baygon, Dursban, Diazinon and Furdan were applied when the aphid population was mainly in the immature feeding stages. Results showed that aphid mortality in the treated plots was no more than in the check plots, clearly indicating the ineffectiveness of the insecticide applications (Bryant 1976c; Hopewell and Bryant 1969).

There are several silvicultural methods that may be utilized to reduce or limit the spread of infestations and restrict damage in infested stands. Destructive cutting or harvesting stands that have relatively new aphid infestations at high population levels has been used with some success in several small areas notably in Terra Nova National Park and near Corner Brook. In these areas all of the noticeably infested fir were cut down and the brush was removed and burned. The aphid still persists but population levels and the incidence of damage have remained low in adjacent stands. Stand fertilization may limit aphid numbers (Thalenhorst 1963; Carrow and Betts 1973; Carrow and Graham 1968; Bryant, Clarke and Bhure 1972) and in addition it could shorten the stand rotation age and thereby reduce the risk of attack. Stand conversion by harvesting followed by prescribed burning of fir reproduction, and replanting or seeding to an aphid resistant tree species, is also a promising method for reducing aphid numbers and the area of aphid susceptible forests (Hall and Richardson 1973). However, the selection of replacement tree species requires examination from various aspects of forestry including the rate of dry matter production, milling and pulping characteristics, site deterioration, susceptibility to other insect and disease conditions, and economics. For example, native black spruce (*Picea mariana* (Mill.) B.S.P.) is a preferred pulpwood species (Fig. 31), but it is slower growing than balsam fir and might cause site deterioration (Damman 1971). Experiments in the replanting of other species of fir have shown that fast-growing Veitch's fir (*Abies veitchii* Lindl.) may be a good species to use on fresh moist sites (Fig. 32, Hall, Singh and Schooley 1971). However, this species may be just as susceptible to hemlock looper and spruce budworm attack as is balsam fir.

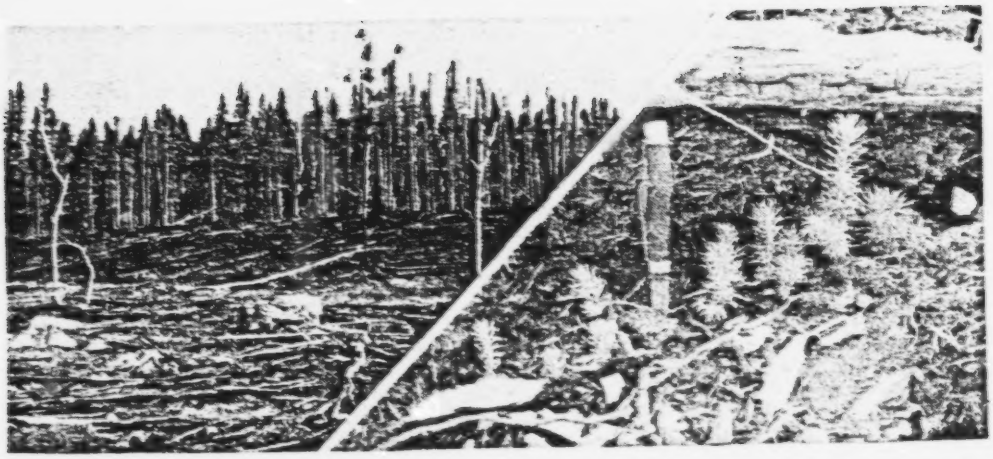

Fig. 31: Prescribed burning followed by seeding to spruce is effective in eliminating balsam fir after a harvest on a productive site.

Fig 32: Veitch's silver fir ten years after planting 2+2 stock.

MANAGEMENT IMPLICATIONS

The balsam woolly aphid is a relatively new insect pest in Newfoundland. However, now that most of the fir forests throughout the Island are infested, the effect of persistent or recurrent damage, rather than initial damage, will be of major importance. Stands that are now infested may continue so for the remainder of their lifetime. However, because the occurrence of aphid populations at a damaging level is cyclic, trees will probably be subjected to alternating periods of damage and recovery. Forest managers should be familiar with the current level of infestation in the balsam fir stands throughout their limits and take problems resulting from balsam woolly aphid attack into consideration when management decisions are made. Detailed records of infestation levels and resulting damage should be kept because information to describe the long term effects of periodically repeated, severe damage on the development of forest stands is not yet available.

The probability of occurrence of damage by an insect pest such as the aphid requires special consideration in determining cutting priorities for harvesting operations. Where economically feasible the most severely damaged forest stands should be harvested first. Dead trees that are not suitable for lumber may still have value as pulpwood. In Newfoundland, trees may be dead for 4 to 5 years before decay causes volume losses that seriously affect the manufacturing of wood pulp.

Severely infested stands should be cut as soon as possible after their discovery. This will reduce the amount of abnormal redwood. Also, for the same reason, stands with severe stem infestation should be cut before stands with crown infestation. Aphids on the stems of trees are particularly detrimental to the production of sawlogs because the redwood they cause is formed in radial bands around the stems. This abnormal wood is considered a grade defect as it causes intensive warping in lumber. The occurence, size, number, and position of these bands in trees should be considered when determining the actual or potential value of a stand for sawlogs and should be a major factor in determining whether a stand should be used for pulpwood or for lumber.

The aphid damage hazard rating system can be used to determine the probability of damage. This system is most meaningful when applied to individual management units where fairly specific inventory information is available. Wherever possible, stands in the highest hazard category should be harvested before those in a lower category. High hazard stands contain mature or overmature balsam fir that are growing on dry or well drained coastal valley-bottom sites. Conducting operations in a fashion that minimizes the number and eliminates concentrations of high hazard stands should have long term beneficial effects.

There is no clearly defined, efficient and environmentally safe method for limiting the abundance of the balsam woolly aphid in forest management areas. Direct control by biological and chemical methods is either ineffective or unacceptable for financial and ecological reasons. However, several treatments to lessen the effects of aphid attack can be applied to young and semi-mature balsam fir stands between the times of establishment and harvest.

Thinning is considered to be an important treatment for young balsam fir stands in areas at high risk to severe damage or tree mortality. It is important to realize that this treatment probably will not reduce the influence of aphid infestation, however, it should reduce the period of exposure to infestation by allowing the trees to reach a merchantable size in a shorter rotation period. It is recommended that wherever possible the balsam fir content of stands should be reduced; desirable non-fir species should not be removed by thinning. Although thinning is possible in semi-mature stands it is not recommended because growth response is less, the residual stands are more susceptible to windthrow, and the disturbance may adversely influence some growth characteristics of the forest site.

Fertilization, especially when applied in combination with thinning in either young or semi-mature stands, should also increase growth rate and shorten the rotation period. However, the effects of fertilizer on aphid population levels and development of damage are not clear and conflicting experimental results have not been resolved.

Balsam fir regeneration, in the moist climatic conditions of Newfoundland, is usually excellent following cutting or natural disturbance. Aphid attack has only a limited effect on seed production and a dense young stand of fir can therefore, be expected to occur on most of the productive sites following normal harvesting, salvage cutting, or aphid-caused mortality. On productive forest sites where the hazard of severe aphid infestation is high, conversion of stands to other tree species is the only recommended way to eliminate the aphid problem. As much of the existing balsam fir regeneration as is possible should be removed by prescribed burning or mechanical means and cleared areas should be seeded or planted to species resistant or non-susceptible to aphid attack. This principle appears simple but there are problems in its application. For example, it would require at least one crop rotation about 60 years to achieve a noticeable change in species composition. Also, this change would have to be implemented over large areas regardless of ownership. Nevertheless, such a program should be initiated as a long-term solution that would reduce forest losses to not only the balsam woolly aphid but also to other insect pests of balsam fir such as the hemlock looper and the spruce budworm.

At the present time, black spruce is the best species to use for replacing balsam fir; it can be established by seeding or planting, is native to Newfoundland, has few insect pests, and is commercially desirable. White spruce is also suitable though it has more insect problems than black spruce. Several other native species, including larch, trembling aspen, and white birch may be suitable from a biological point of view, but are at present little used commercially. A number of exotic species, including *Abies veitchii*, and several spruces, larches and poplars, have also shown early promise for use in Newfoundland but are not yet proven for large-scale use.

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